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EDITORIAL COMMITTEE

JOHN THEODORE BUCHHOLZ

FRED WILBUR TANNER

HARLEY JONES VAN CLEAVE

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JOHN THEODORE BUCHHOLZ

FRED WILBUR TANNER

HARLEY JONES VAN CLEAVE

COMPARATIVE STUDIES ON TREMATODES
(GYRODACTYLOIDEA)
FROM THE GILLS OF NORTH AMERICAN
FRESH-WATER FISHES

WITH FIVE PLATES

BY
JOHN DARY MIZELLE

CONTRIBUTION FROM THE ZOOLOGICAL LABORATORY OF THE
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INTRODUCTION

This investigation was begun originally in the fall of 1933 as a general survey of the parasites of the Centrarchidae of Champaign County, Illinois. After two years of collecting, an attempt was made to identify the monogenetic trematodes, all of which had been preserved in Bouin's solution, before proceeding with the work on the other helminth parasites collected. Due to coagulation of adherent mucus and subsequent adhesion of specimens to the inner surfaces of vials, no Gyrodactyloidea were found in the fluid poured from containers in which specimens had originally been placed. New material was collected and the identification of parasites from living and freshly prepared mounts was undertaken together with the problem of perfecting a suitable technique requisite for research on this group of trematodes. As the work progressed the Monogenea were found to offer such a fertile field for investigation that on March 1, 1936, the problem was restricted to monogenetic forms only and expanded to include hosts of the piscine families Centrarchidae, Seranidae, Cyprinidae, and Poeciliidae from various localities throughout the State of Illinois without restriction to any particular county. A few distribution records from Oklahoma have been made and included in this presentation.

Some of the research covered by this monograph has been briefly presented in three previous papers (Mizelle 1936, 1937, and 1938).

MATERIALS AND METHODS

Due to a lack of time for examination of a large number of fishes collected from several localities on the same date, freezing was resorted to as a means of host preservation. On examination of the branchial material so treated, many of the monogenetic forms present were found free from the host tissues in the containers used for examination. Further work on the efficacy of freezing as a method for the removal of ectoparasitic trematodes from gill tissue resulted in the discovery of an optimum time of exposure ranging anywhere from six to seventy-two hours. In addition to the removal action, freezing also has the simultaneous effects of killing the parasites in a relaxed condition and of breaking up the mucus, both of which facilitate examination and preservation. Exposure for a shorter period than the above-stated minimum fails to break up the mucus to an optimum degree, while over-exposure distorts the specimens.

After freezing, the fishes were thawed in tap water, the gills removed, placed in stoppered homeopathic vials about two-thirds full of tap water, and vigorously shaken between thumb and forefinger for approximately fifty consecutive times. The liquid containing the parasites was then poured into Syracuse watch glasses and alternately diluted and decanted until clear enough for reliable examination with a widefield binocular microscope. The parasites were collected with a capillary pipette equipped with a rubber bulb and transferred to clear water to insure further removal of mucus. Experiments with fifty sets of gills taken from four species of sunfishes, namely, *Helioperca macrochira* (Rafinesque), *Allotis humilis* (Girard), *Xenotis megalotis* (Rafinesque), and *Apomotis cyanellus* (Rafinesque), have shown this method to be effective in removing ninety-two per cent of the gill trematodes present.

For making permanent mounts, the specimens were transferred from watch glasses to slides coated with Mayer's albumen. These were placed on inverted stender dishes in a finger bowl. Alcohol was poured into the container to a level below the top of the stender dishes, the top of the bowl was covered, and the apparatus set in an incubator. It was found that exposure for a period of from one to five minutes (depending upon the amount of water transferred with the parasite to the slide) at a temperature of about fifty-five degrees centigrade was sufficient to coagulate the albumen and securely attach the specimens to the surfaces of the slides. After attachment, the specimens were fixed in either Gilson's or Bouin's fluid and treated subsequently for removal of mercuric salts or picric acid. Specimens were stained in either Ehrlich's acid haemotoxylin, borax carmine, or a mixture of Ehrlich's acid haemotoxylin and Delafield's haemotoxylin in a saturated aqueous solution of potassium alum. It was later discovered that Mayer's albumen was unnecessary and that removal by pipette of the major portion of glycerine and water in which a parasite had been placed on a slide, caused adherence of specimens to the glass surface. Additional adherence was secured by immersing the preparations in fixatives (Gilson's or Bouin's) contained in Coplin jars. Inconsistencies in staining together with poor differentiation and obscuring of structures possessing critical taxonomic value, viz., anchors, bars, hooks, and copulatory apparatus, caused the final abandonment of staining procedures (Mizelle, 1937). Thereafter the specimens were mounted, unstained in balsam. Because of small size and the tendency of the anchors to become entangled in debris and in the cuticula of other specimens, it was found practically impossible to handle these parasites in containers during the ordinary technical processes requisite for mounting. Either of the above procedures for fixation of speci-

mens to slides works very well, but the latter is preferred by the present author because of a shortening of the time element.

The term *haptor* for attachment organs as proposed by Price (1934a) is adopted. The following terms are used as proposed by Mueller (1936): *anchors* for the large hooks of the haptor; *wings* for the membranous structures arising from the convex surfaces of the anchor shafts; *bars* for the chitinous structures connecting the bases of a pair of anchors; and *hooks* for the smaller marginal armature of the haptor. The term *copulatory complex* is used for the ensemble of the male copulatory structures such as the cirrus, accessory piece, cirral thread, and cirral fin when present in combinations of two or more. *Buccal canal* is proposed for the anterior portion of the digestive tube between the pharynx and the opening to the outside.

In forms with nonarticulate bars, the anchor pairs are designated dorsal and ventral, since their shafts curve toward and their points project from the dorsal and ventral haptoral surfaces. In forms with the bars articulate with each other, both pairs of anchors lie on the ventral side of the haptor, and while the designation of the roots is the same, the respective anchors and bars are designated anterior and posterior instead of ventral and dorsal. For ease of reference the two roots comprising the bases of the anchors are designated with regard to the surfaces of the haptor. The root nearest the surface is thus designated the *superficial root* and the other the *deep root*. Mueller (1936) designated the roots of the anchor bases with reference to the anchor points and classified them as internal and external. In his system the inner and outer roots correspond respectively to the roots designated as superficial and deep by the present writer.

The haptoral hooks are numbered consecutively from ventral to dorsal surfaces beginning near the anterior central portion of the haptor and proceeding posteriorly on the ventral side and then anteriorly on the dorsal surface (see figs. 173-174). The two pairs of hooks on the dorsal surface are numbered six and seven, number six being the more posterior. The hooks of pair number five are usually situated nearer the ventral than the dorsal surface. They may lie between the bars or between the distal ends of the ventral anchor shafts.

Descriptions of forms in this work have been made on living specimens as well as on stained and unstained mounts. Sections were made of *Cleidodiscus robustus* Mueller, 1934, and *Cleidodiscus capax* Mizelle, 1936. Measurements do not follow surfaces of curved structures, but have been made across the arcs formed by them. For example, an anchor length consists of a measurement extending from the region of junction

(curved portion) of the shaft and point to the tip of the more distant root of the anchor base.

All measurements, except those of the anchors, hooks, bars, and cirri were taken on freshly killed specimens temporarily mounted in a solution of equal parts of glycerine and water, on glass slides without cover-glasses. Measurements of the anchors, hooks, bars, and cirri were made with coverglasses on the preparations. Each mean measurement given in this work is a calculated average derived from measurements taken from twenty different specimens.

After considerable research on this group of parasites (Tetraonchinae and Dactylogyrinae) a modification of the relative importance and treatment of different structures was made with reference to their taxonomic value. In the first part of the work the haptoral hooks were measured individually, but no figures of these structures were given. In later parts of the investigation the hook measurements are usually represented by minima and maxima for the total number of hooks present, and descriptions for these are supplemented (except *Actinocleidus fergusonii* n. sp.) by one or more figures to illustrate the extent of differentiation of parts. In similar manner the cirrus descriptions have been supplemented by measurements which were omitted in the earlier portion of the investigation. It should be pointed out that species described herein are arranged according to genera and not with reference to chronological completion of descriptions. Since the general internal structure in the subfamilies Tetraonchinae and Dactylogyrinae is very similar, figures of whole specimens are not given for all the species described. Structures considered to possess critical taxonomic value are figured for all the forms described in this work.

Type material (cotypes) of forms described herein have been deposited in the U. S. National Museum Helminthological Collection.

ORDER MONOGENEA CARUS, 1863

HISTORICAL REVIEW

The group Trematoda, named by Rudolphi in 1808, as an order, originally included the following genera: *Monostomata* Zeder, *Amphistomata* Rudolphi, *Distoma* Retzius, and *Polystoma* Zeder. In 1858, van Beneden proposed the term monogénèses for trematodes which develop without metamorphosis and digénèses for those which develop with metamorphosis, the former category generally consisting of ectoparasites and the latter exclusively of endoparasites. In 1863, Carus proposed the terms Monogenea and Digenea, respectively, to replace the two terms of van

Beneden. In 1892, Monticelli divided the order Trematoda into the suborders Heterocotylea, Aspidocotylea, and Malacocotylea. The suborder Heterocotylea coincides with the Monogenea (Pratt, 1900). The Aspidocotylea and Malacocotylea are divisions of the Digenea. Odhner (1912) divided the Monogenea of Carus into the Polyopisthocotylea and Monopisthocotylea, respectively, on the basis of the presence or absence of a genito-intestinal canal.

According to Fuhrmann (1928), as set forth in Kükenthal's *Handbuch der Zoologie*, the Monogenea and Digenea of Carus are accepted as orders and the order Trematoda Rudolphi, is elevated to the status of class. The order Monogenea Carus, as given by Fuhrmann, embraces three suborders, Monopisthodiscinea, Monopisthocotylinea, and Polyopisthocotylinea. The suborder Monopisthodiscinea is divided into four families, Progyrodactylidae Johnston and Tiegs, 1922, Gyrodactylidae Cobbold, 1877, Dactylogyridae Bychowsky, 1933, and Calceostomatidae (Parona and Perugia, 1890). The suborder Monopisthocotylinea contains three families, Udonellidae Taschenberg, 1879, Monocotylidae Taschenberg, 1879, and Tristomidae van Beneden, 1858, while the suborder Polyopisthocotylinea is divided into five families, namely, Polystomidae van Beneden, 1858, Microcotylidae Taschenberg, 1879, Octocotylidae van Beneden and Hesse, 1863, Onchocotylidae Cerfontaine, 1899, and Diclidiphoridae Cerfontaine, 1894.

Price (1937a) prefers the divisions Monopisthocotylea (= Monopisthodiscinea and Monopisthocotylinea) and Polyopisthocotylea (= Polyopisthocotylinea) of Odhner to those of Fuhrmann and designates the superfamilies Gyrodactyloidea Johnston and Tiegs, 1922, and Capsaloidea Price, 1937, respectively, to replace the suborders Monopisthodiscinea and Monopisthocotylinea of Fuhrmann. Price's classification is followed in the present publication.

KEY TO THE SUBORDERS OF MONOGENEA CARUS

- Genito-intestinal canal wanting; haptor with or without a large sucking disc..
 Monopisthocotylea Odhner
 Genito-intestinal canal present; haptor with separate suckers.....
 Polyopisthocotylea Odhner

KEY TO THE SUPERFAMILIES OF MONOPISTHOCOTYLEA ODHNER, 1912

- Posterior haptor armed; anchors with supporting bars.....
 Gyrodactyloidea Johnston and Tiegs
 Posterior haptor armed or unarmed; when armed, anchors without supporting
 bars..... Capsaloidea Price

SUPERFAMILY GYRODACTYLOIDEA JOHNSTON
AND TIEGS, 1922

GENERAL MORPHOLOGY OF THE GYRODACTYLOIDEA

Changes in classification, since the characterization of this superfamily by the above authors, have made it necessary to revise parts of their description. The description of the reproductive system, however, is taken from their monograph.

General anatomy.—The superfamily Gyrodactyloidea contains forms found in or on fishes, amphibians, and cephalopods. The species are characterized by the absence of anterior haptors and suckers of the ordinary type. A posterior haptor is present and consists of an armed disc which may or may not be distinctly set off from the body of the parasite. The haptor possesses hooks only (Isancistrinae), or hooks and anchors (one or two pairs) whose bases are connected by chitinous bars. The relationships of elements of haptoral armature vary greatly in different groups. Eye spots may be present or absent. In the pharyngeal region there are masses of glandular tissue which open to the outside by structures called *head organs* by Johnston and Tiegs (1922). An exception to this condition occurs in the family Calceostomatidae, in which these glands open by small ducts not concentrated in groups to form the so-called head organs.

Reproductive system.—"The testis is a compact or only slightly lobed organ, single or double, and never lies anterior to the ovary. The vas deferens may be a simple tube hardly expanded into a vesicula seminalis, or it may be widely dilated; sometimes enormously so in the Australian species. A bulbous ejaculatorius may or may not be present. The cirrus may range from a simple chitinous tube to a structure of considerable complexity, while an accessory clasping apparatus may occur.

"The ovary may be a branched or unbranched organ, lying either in the midline or asymmetrically. A vagina may be present (single or double) or absent; and there may be a receptaculum seminis connected with it.

"Shell-glands may vary from simple glandular thickenings of the oötype, to very prominent glands connected by long ducts with the female duct. The female aperture usually lies immediately behind the male opening, but sometimes at a considerable distance from it, generally laterally. Never more than one egg is present in the uterus. The egg may be laid, or it may be retained in the uterus to develop into a young worm which may, while *in utero*, produce a second generation.

"The yolk system may be poorly or strongly developed. In the most primitive members of the group there is a very distinct communication between the yolk system and the intestine in the posterior region of the animal."

Digestive and excretory systems.—The mouth opens into a short buccal canal which empties into a muscular pharynx. An esophagus may or may not be present. The intestine may be saccate or bifurcate to form two crura which may or may not possess caeca. The crura may end blindly or be confluent with each other in the posterior body regions.

Johnston and Tiegs (1922) state, "Excretory ducts open either at the anterior end or, in some forms, probably at the posterior end." In the Dactylogyrinae and Tetraonchinae the present author is sure of excretory openings only in the anterior regions at about the level of the copulatory complex (see page 17).

KEY TO THE FAMILIES OF GYRODACTYLOIDEA

1. Viviparous.....Gyrodactylidae Cobbold
Oviparous.....2
2. Vitello-intestinal duct present.....Protogyrodactylidae Johnston and Tiegs
Vitello-intestinal duct wanting.....3
3. Anterior end of body expanded to form head lappets.....
.....Calceostomatidae (Parona and Perugia)
Anterior end of body not expanded to form head lappets.....
.....Dactylogyridae Bychowsky

THE NORTH AMERICAN FRESH-WATER GYRODACTYLOIDEA

REVIEW OF TAXONOMIC LITERATURE

Specific taxonomic investigations concerning the Gyrodactyloidea from North American fresh-water fishes have been meager.¹ Most important are the works of Mueller (1934, 1936, 1936a, 1937, 1937a, 1938), Mueller and Van Cleave (1932), Van Cleave (1921), Van Cleave and Mueller (1932 and 1934), and Price (1937a). In 1934 Mueller created the genera *Cleidodiscus* and *Urocleidus*; in 1936 he created the genera *Onchocleidus*, *Leptocleidus*, *Tetracleidus*, and *Aristocleidus*; and in 1937 he created the additional genera *Haplocleidus*, *Pterocleidus*, and *Actinocleidus*. The established genus *Ancyrocephalus* was made to include strictly marine forms (Mueller, 1936) and certain fresh-water Tetraonchinae of uncertain generic relationships.

¹The major portion of the work on the American fresh-water Gyrodactyloidea has dealt with control measures and identification only to genus. A literature review of this work will be found in the section of this publication dealing with economic importance.

The present author (Mizelle, 1936) described twelve species of Tetraonchinae from the gills of Illinois Centrarchidae and Serranidae. In 1937 he described three species of Dactylogyrinae from the blunt-nosed minnow, *Hyborhynchus notatus*, and at present has descriptions of four additional species of Tetraonchinae and one species of Dactylogyrinae in press. Another species of Tetraonchinae (*Actinocleidus fergusoni*) is originally described herein. The six last mentioned forms will be listed as new species in this publication. Including all the forms in the above taxonomic categories, the described species of North American fresh-water Gyrodactyloidea now total sixty-one. Three of these, namely, *Tetraonchus monenteron* (Wagener, 1857), *Dactylogyrus anchoratus* (Dujardin, 1845), and *Gyrodactylus elegans* von Nordmann, 1832, were first described from another continent (Europe). Seven of these belong to the Gyrodactylinae (genus *Gyrodactylus*), six to the Dactylogyrinae (genus *Dactylogyrus*), forty-seven to the Tetraonchinae, (12 *Cleidodiscus*, 11 *Onchocleidus*, 9 *Actinocleidus*, 3 *Haplocleidus*, 3 *Pterocleidus*, 3 *Urocleidus*, 2 *Tetraonchus*, 1 *Leptocleidus*, 1 *Aristocleidus*, 1 *Tetracleidus*, and 1 *Ancyrocephalus*), and one to the subfamily Lepidotrematinae, viz., *Lepidotes collinsi* Mueller, 1936.

Price (1937a) lists forty-five Dactylogyrinae and nine Gyrodactylinae as foreign species (mostly European). Mueller (1936) gives six as the number of European species of fresh-water Tetraonchinae. According to the above information, the species of Gyrodactylinae are about evenly distributed between North America and Europe, whereas most of the Dactylogyrinae are found in Europe and most of the Tetraonchinae in North America.¹

KEY TO THE SUBFAMILIES OF GYRODACTYLIDAE COBBOLD, 1877

- Haptor with two anchors and 16 hooks.....Gyrodactylinae Monticelli
Haptor without anchors but with 15 hooks.....Isancistrinae Fuhrmann

KEY TO THE SUBFAMILIES OF DACTYLOGYRIDAE BYCHOWSKY, 1933

1. Haptor with 2 pairs of anchors.....2
Haptor with 1 pair of anchors.....3
2. Haptor with a pair (dorsal and ventral) of accessory structures or squamodiscs
.....Diplectaninae Monticelli
Haptor without squamodiscs.....Tetraonchinae Monticelli
3. Haptor with a circle of heavy cuticularized, tubular structures.....
.....Bothitrematinae Price
Haptor without chitinized tubular structures.....Dactylogyrinae Bychowsky

¹After this publication went to press Mueller (1938) described additional species of Tetraonchinae and Dactylogyrinae.

GENERAL MORPHOLOGY OF THE NORTH AMERICAN FRESH-WATER
TETRAONCHINAE MONTICELLI, 1903

General anatomy.—The flattened body comprises two distinctly tandem regions, an anterior, very narrowly elliptical, body proper and a posterior, hexagonal or discoidal haptor.¹ The body surface is devoid of scales (except in some specimens of *Cleidodiscus robustus* Mueller, 1934). Internal monaxon spicules are very infrequently found in the body parenchyma, namely, in some specimens of *Cleidodiscus robustus* and *Cleidodiscus capax* Mizelle, 1936. A pair of lateral lobe-like projections (cephalic lobes) are generally present in the head region. Two pairs of eye spots are present, located dorsally near the anterior end, with one pair behind the other, those of the anterior pair being generally smaller. Each eye spot is composed of an aggregation of melanistic granules which are easily separated from each other by cover-glass pressure. A group of glandular cells occurs on each side of the body in the region of the pharynx. These glands open to the exterior by head organs situated on the anterolateral margins of the cephalic region.

Four anchors always present on the haptor, generally similar in shape (except genus *Aristocleidus* Mueller, 1936) and size (except genus *Haplocleidus* Mueller, 1937). Each anchor is differentiated into a base, which is usually bifurcate to form two roots; a shaft which may be solid or hollow; and a point which projects from the surface of the haptor. The shaft may be regularly recurved distally, merging imperceptibly with the point or sharply recurved to form a distinct internal angle at this locus. Membranous wings, so designated by Mueller (1936), arise from the convex surfaces of the anchor shafts. These have been found universally present in the species described in this investigation. However, these structures exhibit differential development and are often scarcely perceptible in some species. Two bars always present (except in the genera *Tetraonchus* and *Murraytrema*), each of which connects the bases of a pair of anchors. The bars generally exist as separate structures. *Actinocleidus* Mueller, 1937, is the only genus in which the bars are articulated with each other. Seven pairs of chitinous hooks (eight pairs in *Tetraonchus*) are generally present on the haptor. A hook may be a solid or a hollow, cylindrical, tapering rod ending distally in a sickle-shaped process and opposable piece, or a solid structure distinctly differentiated into a base, shaft, sickle-shaped termination and an opposable piece. Five pairs of hooks are located ventrally and two pairs dorsally (see figs. 173-174).

¹Due to contraction at death, the postero-lateral sides of a haptor, normally hexagonal, may be pulled together to the extent that the posterior side is obliterated and in such case the structure assumes a pentagonal shape. The junction of the haptor with the body is considered one side of the haptor. Body contraction at death may shorten or accentuate the peduncle so that relative separation of haptor from the body becomes a poor descriptive character.

Reproductive system.—The single testis, regular in outline, is located in the posterior half of the body and may be dorsal, posterior, or postero-dorsal to the ovary. The vas deferens passes forward, generally, on the left side of the body, and usually dilates to form a seminal vesicle immediately posterior to the cirrus base. Two prostate glands generally present, situated near the posterior end of the copulatory complex, and each connected with the cirrus by a single individual duct. The prostate glands are similar to those described by Goto (1894) for the genus *Epibdella*. The copulatory complex consists of a cirrus and one or more of the following chitinous structures: solid accessory piece, cirral thread, and cirral fin. This compound structure is situated in a vestibule immediately in rear of the esophageal bifurcation. The cirrus projects or empties ventrally through the vestibular pore.

The ovary is a nonlobed organ with spatial relationships with the testis as given above. It may be larger or smaller than or about the same size as the testis. Internally it is filled with relatively large, clear, nucleated eggs of different sizes, which are easily visible in living mounts. The eggs diminish in size toward the posterior portion of the ovary. The oviduct arises from the anterior portion of the ovary and passes forward near the midline of the body. Never more than one egg has been observed in the oviduct at a given time. The egg pore is situated ventrally near the vestibular pore. The single vagina (wanting in the genus *Urocleidus* and also in species of other genera) may occur on either lateral body margin. It is generally provided with a chitinous tube which connects it with a seminal receptacle, situated near the anterior end of the ovary. The vitellaria consist of innumerable minute follicles arranged in two lateral longitudinal bands extending from dorsal to ventral body surfaces. Anteriorly these bands may or may not be confluent immediately behind the pharynx near their anterior limits but are always broadly confluent posteriorly on or near the peduncle. Encroachment of the vitellaria on the midbody regions of old individuals may become so marked as to obscure the visibility of internal organs. Vitelline ducts enter the oötype one on each side just anterior to the ovary as described by Goto (1894) for the genus *Tristomum* Cuvier, 1817, and by MacCallum (1915) for *Ancyrocephalus teuthis*.

Digestive and excretory systems.—The mouth is located in the mid-ventral region near the level of the anterior eye spots. A short buccal canal passes posterodorsad to enter the well-developed pharynx. The short esophagus bifurcates (except in *Tetraonchus*) to form two lateral intestinal crura which unite posteriorly (except in *Murraytrema*) in the region of confluency of the vitellarial bands.

The excretory system consists of a maze of ramifying tubules pre-

sumably terminating in flame cells. Basically a single pair of lateral collecting ducts (one on each side) occurs in the posterior part of the anterior body half. Anteriorly each tube bifurcates to form two ducts. One of these passes laterally at an angle of about forty-five degrees and empties on the dorsolateral body surface, near the level of the copulatory complex. The other passes anteriorly and terminates lateral to the anterior eye spot.¹ Posteriorly the single duct referred to above bifurcates in the region of the ovary to form two tubes which pass posteriorly, turn mesiad in the region of confluency of the vitellarial bands and unite to form a short tube. This structure unites with its bilateral mate to form a single duct which terminates near or on the peduncle. Especially large solenocytes have been observed in some species between the level of the ovary and the base of the copulatory complex. Flame cell numbers and patterns have not been worked out for the group.

Note.—The status of most of the following genera is uncertain at the present time. The genera *Onchocleidus*, *Tetracleidus*, *Aristocleidus*, *Haplocleidus*, *Pterocleidus*, and *Urocleidus* are probably synonymous.

KEY TO THE GENERA OF NORTH AMERICAN
FRESH-WATER TETRAONCHINAE
(Excluding *Tetraonchus* and *Murraytrema*)

1. Cirrus relatively simple.....2
Cirrus in a large coil.....*Leptocleidus* Mueller
2. Anchors similar in shape.....3
Anchors dissimilar in shape.....*Aristocleidus* Mueller
3. Anchors similar in size.....4
Anchors markedly dissimilar in size.....*Haplocleidus* Mueller
4. Bars nonarticulate.....5
Bars articulate with each other.....*Actinocleidus* Mueller
5. Vagina present.....6
Vagina wanting.....*Urocleidus* Mueller
6. Vagina on right body margin.....7
Vagina on left body margin.....*Cleiaodiscus* Mueller
7. Anchor shafts without spurs.....8
Anchor shafts with spurs.....*Pterocleidus* Mueller
8. Accessory piece present.....*Tetracleidus* Mueller
Accessory piece wanting.....*Onchocleidus* Mueller

¹The present author (Mizelle, 1936) observed what he interpreted to be excretory pores in the anterior and posterior regions of these parasites as mentioned by Johnston and Tiegs (1922). Further observations have failed to reveal these structures consistently, so that it seems best to avoid any detailed discussion of them at the present time.

Genus *Cleidodiscus* Mueller, 1934

Diagnosis.—Tetraonchinae with intestine bifurcate but confluent posteriorly. Vagina present on the left body margin about midway the length. Copulatory complex consisting of a cirrus and accessory piece. Accessory piece well developed, always present and articulated to the cirrus base. Haptor distinct, discoidal, pentagonal, or hexagonal in shape. Two separate bars present, each of which connects the bases of members of a pair of anchors. Each of the fourteen hooks present is structurally differentiated into a base, shaft, sickle-shaped termination, and opposable piece. Parasitic on the gills of fresh-water fishes. Type species, *Cleidodiscus robustus* Mueller, 1934.

Cleidodiscus robustus Mueller, 1934

Figs. 1, 13-21

Hosts and Localities: Bluegill Sunfish (*Helioperca macrochira*), Illinois River, Havana, Ill.; Chautauqua Lake, Havana, Ill.; Horseshoe Lake, Cairo, Ill.; Lake Decatur, Decatur, Ill.; Lake Senachwine, Henry, Ill.—Green Sunfish (*Apomotis cyanellus*), Embarrass River, Urbana, Ill.

Location: Gills.

Specimens: U.S.N.M. Helm. Coll. No. 9090.¹

Synonym: *Cleidodiscus incisor* Mizelle, 1936.

General anatomy.—Relatively large parasites whose surfaces often possess chitinous scale-like structures. The parenchyma of old individuals very frequently contains monaxon spicules. Average length 1.414 mm. (0.615-2.296 mm.), average width at level of cephalic lobes 0.132 mm. (0.106-0.246 mm.), average greatest body width 0.216 mm. (0.121-0.410 mm.), average width of peduncle at junction with haptor 0.060 mm. (0.041-0.106 mm.). Haptor distinct, discoidal, and broader than long, average width 0.111 mm. (0.092-0.148 mm.), average length 0.106 mm. (0.082-0.139 mm.). Ventral bar similar in shape to dorsal bar but slightly longer. Average length of ventral bar 0.028 mm. (0.025-0.032 mm.), average length of dorsal bar 0.027 mm. (0.024-0.029 mm.). Anchors similar in shape, bases bifurcate, superficial roots about same length as knob-like deep roots. Wings present on anchor shafts but often so delicate as to be scarcely perceptible. Shafts of both pairs of anchors hollow and regularly recurved, making junction with the points without formation of an angle. Ventral anchors slightly longer than dorsal anchors, bases of the two pairs of anchors approximately the same width. Average length of ventral anchors 0.026 mm. (0.021-0.030 mm.), average width 0.012 mm. (0.010-0.017 mm.), average length of dorsal anchors 0.024 mm. (0.019-0.027 mm.), average width of dorsal anchors

¹These specimens were deposited as cotypes of *C. incisor*, which is now a synonym of *C. robustus*.

0.012 mm. (0.009-0.017 mm.). Hook bases ovate and very short as compared with lengths of shafts. Hooks of pair number one slightly shorter than rest of hooks. The arrangement of the hooks is characteristic of North American fresh-water Tetraonchinae possessing fourteen haptorial hooks (see pages 9, 15, and 62).

<i>Hook pair</i>	<i>Average length in mm.</i>	<i>Range in mm.</i>
1	0.015	0.013-0.017
2	0.017	0.015-0.020
3	0.019	0.016-0.023
4	0.019	0.017-0.023
5	0.016	0.014-0.017
6	0.019	0.017-0.021
7	0.019	0.017-0.023

Anterior eye spots smaller and usually closer together than the members of the posterior pair.

Reproductive system.—Gonads near middle of body, testis ovate and located posterior to ovary. Vas deferens passes forward on left side of body and expands to form a conspicuous seminal vesicle just posterior to cirrus base. Only one prostate gland has been observed. It is bulb-shaped, located posterior to the cirrus base and contains a coarsely granular yellowish fluid. It empties into cirrus base by a single duct arising from the anterior end. Copulatory complex well developed and situated in a relatively large vestibule. Cirrus a simple, curved, chitinous tube; accessory piece a blade-like chitinous structure with a knob near the middle, which serves as a site for attachment of muscles. Contractile elements arise on posterior surface of knob of accessory piece and insert on base of cirrus. On contraction of these structures the cirrus and accessory piece separate distally and the cirrus is projected ventrally, for a short distance, through the pore of the vestibule. Retraction mechanism of the cirrus not understood.

Ovary ovate in shape, smaller than testis, and situated anterior to it. Egg pore located on ventral surface on right of copulatory complex. Vagina present on left side, near junction of first and second thirds of body length; vaginal canal short, with a row of spines encircling the base at its junction with the large pyriform seminal receptacle. Vitellaria and vitelline ducts as described in the general morphology of North American fresh-water Tetraonchinae. Shell gland a cluster of glandular cells surrounding the oötype.

Digestive and excretory systems.—Digestive and excretory systems as given in the general morphology of the North American Fresh-water Tetraonchinae. Average diameter of pharynx 0.076 mm. (0.046-0.123 mm.).

Systematic position.—In the present investigation this parasite has been taken only from the bluegill and green sunfishes. It occurs in mixed infestations on the former host with *Pterocleidus acer* (Mueller, 1936), *Haploleidus dispar* (Mueller, 1936), *Actinocleidus fergusonii* n. sp., and *Onchocleidus mucronatus* Mizelle, 1936, and in mixed infestations on the latter host with *Cleidodiscus diversus* n. sp., *Actinocleidus longus* n. sp., *Onchocleidus cyanellus* n. sp., and an undescribed member of the genus *Actinocleidus* Mueller, 1937. This form was described by the present author (Mizelle, 1936) as *Cleidodiscus incisor*. Study of Mueller's type specimens revealed it to be a synonym of *Cleidodiscus robustus*.

One hundred per cent infestation with *C. robustus* was recorded for: nineteen bluegill sunfish from Chautauqua Lake, Havana, Ill., in May, 1936; thirty-one bluegills from the Illinois River, Havana, Ill., in May, and June, 1936; six bluegills from Horseshoe Lake, Cairo, Ill., in June, 1936; twenty-three bluegill sunfish from Lake Decatur, Decatur, Ill., in June, July, and August, 1936. Fourteen bluegills from Lake Senachwine, Henry, Ill., were found only fifty per cent infested with this gill parasite in June, 1936. The green sunfish is only occasionally infested with this helminth.

Cleidodiscus capax Mizelle, 1936

Figs. 7, 67-75

Hosts and Localities: White Crappie (*Pomoxis annularis*), Lake Decatur, Decatur, Ill.; Illinois River, Havana, Ill.—Black Crappie (*Pomoxis sparoides*), Lake Senachwine, Henry, Ill.; Illinois River, Havana, Ill.

Location: Gills.

Specimens: U.S.N.M. Helm. Coll. No. 9079.

General anatomy.—Relatively large gill parasites devoid of surface scales but often possessing internal monaxon spicules in the parenchyma. Average length 1.603 mm. (0.959-2.050 mm.), average width at level of cephalic lobes 0.161 mm. (0.115-0.205 mm.), greatest body width average 0.301 mm. (0.180-0.410 mm.), average width of peduncle at junction with haptor 0.096 mm. (0.082-0.107 mm.). Haptor distinct, discoidal in outline and broader than long, average width 0.158 mm. (0.115-0.180 mm.), average length 0.106 mm. (0.090-0.123 mm.). Ventral bar heavier and slightly longer than dorsal bar. Average length of ventral bar 0.032 mm. (0.028-0.034 mm.), average length of dorsal bar 0.030 mm. (0.024-0.036 mm.). Anchors similar in shape, bases often nonbifurcate, obscuring the two roots which are always evident in young individuals. Wings of anchor shafts often so delicate as to be scarcely perceptible. Shafts of both pairs of anchors solid and regularly recurved without formation of an angle at the point of junction with their respective points. Ventral anchors larger than dorsal anchors, bases of ventral anchors markedly wider than bases of dorsal anchors. Average length of ventral anchors 0.032 mm. (0.026-0.038 mm.), average width 0.027 mm. (0.019-0.036 mm.), average length

of dorsal anchors 0.031 mm. (0.026-0.038 mm.), average width 0.023 mm. (0.019-0.029 mm.). Hook bases ovate and very short as compared with lengths of shafts. Hooks of pair number one shorter than the rest of the hooks. The arrangement of the hooks is characteristic of North American fresh-water Tetraonchinae possessing fourteen haptorial hooks (see pages 9, 15, and 62).

<i>Hook pair</i>	<i>Average length in mm.</i>	<i>Range in mm.</i>
1	0.014	0.013-0.017
2	0.016	0.013-0.019
3	0.017	0.014-0.019
4	0.018	0.015-0.019
5	0.016	0.013-0.019
6	0.017	0.013-0.019
7	0.017	0.013-0.019

The anterior eye spots are smaller and invariably farther apart than members of the posterior pair.

Reproductive system.—Gonads situated near the middle of the body, testis ovate and situated posterior to ovary. Vas deferens passes forward on left side of body and expands to form a fusiform seminal vesicle near the cirrus base. Prostate glands two in number, larger one somewhat fusiform in shape and filled with a finely granular colorless fluid, smaller one subpyriform in outline and filled with a coarsely granular yellowish fluid. Copulatory complex well developed and situated in a relatively small vestibule. Cirrus a curved chitinous tube reciprocally coiled about the accessory piece. Accessory piece a curved chitinous rod. A conspicuous knob which serves as a site for muscular attachment occurs on the anterior portion of the accessory piece. Contractile elements arise on posterior portion of this knob and insert on the cirrus base. On contraction of these structures the anterior portion of the accessory piece remains *in situ*, the portion of the accessory piece posterior to the knob bends in an elbow fashion and the cirrus is projected through the vestibular pore for a distance equal to about one half its length. The terminal portion of the accessory piece serves as a guide for the cirrus. Presumably, the retraction of the cirrus is accomplished by straightening of the accessory piece.

Ovary ovate, smaller than testis and situated anterior to it. Egg pore on ventral surface, on right of copulatory complex base. Vagina present on left body margin, anterior to middle of body proper; vaginal canal a long chitinous tube connecting vagina with the well-developed seminal receptacle. Vitellaria and vitelline ducts as described in the general morphology of the North American fresh-water Tetraonchinae. Shell gland a cluster of glandular cells surrounding the oötype.

Digestive and excretory systems.—The digestive and excretory sys-

tems are as described in the general morphology of the North American fresh-water Tetraonchinae. Average diameter of pharynx 0.139 mm. (0.082-0.164 mm.).

Systematic position.—This parasite has been found to occur in heavy infestations on the gills of the black crappie from Lake Senachwine, Henry, Ill. Another form, *Cleidodiscus vancleavei* Mizelle, 1936, also occurs on the same host, but the two species have not been recovered from the same host specimen. *Cleidodiscus capax* occurs in smaller numbers on the gills of the white crappie, in mixed infestations with *Cleidodiscus longus* Mizelle, 1936, *Cleidodiscus uniformis* Mizelle, 1936, and *Cleidodiscus vancleavei*. In size, this form closely approximates that of *Cleidodiscus robustus* Mueller, 1934, but the anchors, bars, copulatory complex, and vagina are morphologically different from corresponding structures in *C. robustus*. *C. capax* occurs only on the black and white crappies, whereas *C. robustus* has been taken from the pumpkinseed, bluegill, green sunfish, "sunfish," and "bass" (Mueller, 1936). Tetraonchid parasites of crappies (black and white) have not been found to occur on other hosts in this investigation. One hundred per cent infestation with *C. capax* was recorded for: forty-eight white crappies from Lake Decatur, Decatur, Ill., in May, June, July, and August, 1936; sixteen black crappies from Lake Senachwine, Henry, Ill.; and five black crappies from the Illinois River, Havana, Ill., in June, 1936.

Cleidodiscus longus Mizelle, 1936

Figs. 4, 49-56

Hosts and Localities: White Crappie (*Pomoxis annularis*), Lake Decatur, Decatur, Ill.; Salt Fork of the Big Vermilion River, south of Oakwood, Ill.; Boomer Creek, Stillwater, Okla.

Location: Gills.

Specimens: U.S.N.M. Helm. Coll. No. 9080.

General anatomy.—Relatively small parasites devoid of surface scales and internal spicules. Average length 0.626 mm. (0.492-0.713 mm.), average width at level of cephalic lobes 0.087 mm. (0.066-0.107 mm.), greatest body width average 0.106 mm. (0.098-0.123 mm.), average width of peduncle at junction with haptor 0.064 mm. (0.038-0.086 mm.). Haptor distinct, hexagonal in shape, and broader than long, average width 0.110 mm. (0.076-0.123 mm.), average length 0.100 mm. (0.057-0.114 mm.). Ventral bar with notched ends, relatively straight, heavier and slightly longer than dorsal bar which is bent in middle to present a sagged appearance. Average length of ventral bar 0.038 mm. (0.032-0.042 mm.), average length of dorsal bar 0.037 mm. (0.028-0.042 mm.). Anchors similar in shape, bases bifurcate, superficial roots longer than deep roots. Wings on anchor shafts clearly discernible. Distal portion

of each anchor shaft markedly dilated and containing a cavity which extends into basal portion of each point. Anchor points and shafts unite to form an internal angle at locus of junction. Ventral anchors larger than dorsal anchors. Average length of ventral anchors 0.043 mm. (0.038-0.051 mm.), average width 0.028 mm. (0.019-0.032 mm.), average length of dorsal anchors 0.037 mm. (0.031-0.046 mm.), average width 0.017 mm. (0.013-0.023 mm.). Bases of ventral anchors conspicuously wider than bases of dorsal anchors. Hook bases of pair number five ovate and shorter than their respective shafts, bases of other hooks elongate-ovate and about same length as their shafts. Hooks of pair number five noticeably shorter than rest of hooks. The arrangement of the hooks is characteristic of North American Tetraonchinae possessing fourteen haptor al hooks (see pages 9, 15, and 62).

<i>Hook pair</i>	<i>Average length in mm.</i>	<i>Range in mm.</i>
1	0.017	0.015-0.019
2	0.020	0.017-0.023
3	0.021	0.019-0.023
4	0.019	0.017-0.023
5	0.014	0.009-0.017
6	0.019	0.015-0.021
7	0.021	0.017-0.023

The anterior eye spots are smaller and invariably farther apart than members of the posterior pair.

Reproductive system.—Gonads located anteriorly in posterior half of body, testis elongate and located posterior to ovary. Vas deferens arises from anterior end of testis, passes forward on left side of body without evident dilatation to form a seminal vesicle. Two prostate glands present, larger one elongate-saccate in outline and filled with a finely granular colorless fluid, the smaller one saccate and containing a coarsely granular yellowish fluid. Each prostate gland empties into base of cirrus by a single individual duct. Copulatory complex well developed and situated in a slender vestibule. Cirrus a long chitinous whip-like tube attenuated distally to a fine thread. Accessory piece consists of a chitinous structure with a deep groove which serves as a guide for the cirrus. Contractile elements originate on the accessory piece near its midportion and insert on the base of the cirrus. On contraction of these elements, the portion of the accessory piece distal to the muscular attachments remains *in situ*, the proximal portion bends in elbow fashion and the cirrus is projected through the vestibular pore, beyond the body surface, for a distance equal to about one-half its length. Presumably, the straightening of the accessory piece retracts the cirrus.

Ovary ovate, from one to two times as large as testis and situated anterior to it. Uterine pore located on ventral surface at right of copula-

tory complex base. Vagina present on left margin near the middle of the body; vaginal canal a chitinous tube emptying mesially into a well-defined seminal receptacle. The vitellaria and vitelline ducts are as described in the general morphology for the North American fresh-water Tetraonchinae. Shell gland, a group of glandular cells surrounding the oötype.

Digestive and excretory systems.—The digestive and excretory systems exist as described in the general morphology of the North American fresh-water Tetraonchinae. Average diameter of pharynx 0.033 mm. (0.030-0.036 mm.).

Systematic position.—This species of gill parasite has been recovered only from the white crappie in this investigation. It occurs in mixed infestations with *Cleidodiscus vancleavei* Mizelle, 1936, *Cleidodiscus capax* Mizelle, 1936, and *Cleidodiscus uniformis* Mizelle, 1936. *Cleidodiscus longus* possesses a copulatory complex similar to but longer than that of *C. uniformis*. The vaginae of the two species are almost identical. The chief differences are the dissimilarities of bars and anchors of these two species. The bases of the two pairs of anchors of *C. longus* are markedly different in width, whereas the widths of the two pairs of anchors of *C. uniformis* are almost identical. Average width of ventral anchors of *C. longus* 0.028 mm., average width of dorsal anchors 0.017 mm. Average width of ventral anchors of *C. uniformis* 0.017 mm., average width of dorsal anchors 0.016 mm. *C. longus* possesses anchors whose shafts are markedly dilated distally while the anchors of *C. uniformis* are never more than slightly dilated. Each anchor shaft of *C. longus* meets its respective point to form an internal angle, but the shafts of *C. uniformis* are uniformly recurved without formation of an angle at this point.

The bars of the two species are different and constant in shape. *C. uniformis* is the closest morphological relative of *C. longus*.

Forty-eight white crappies from Lake Decatur, Decatur, Ill., in May, June, July, and August, 1936, were infested one hundred per cent with this gill parasite. Only one host was taken from the Salt Fork of the Big Vermilion River south of Oakwood, Ill., July, 1936. Five hosts from Boomer Creek, Stillwater, Okla., were infested one hundred per cent with this species.

Cleidodiscus uniformis Mizelle, 1936

Figs. 12, 85-93

Hosts and Localities: White crappie (*Pomoxis annularis*), Lake Decatur, Decatur, Ill.; Salt Fork of the Big Vermilion River, south of Oakwood, Ill.; Boomer Creek, Stillwater, Okla.

Location: Gills.

Specimens: U.S.N.M. Helm. Coll. No. 9081.

General anatomy.—Relatively small parasites devoid of surface scales and internal spicules. Average length 0.583 mm. (0.398-0.738 mm.), average width at level of cephalic lobes 0.080 mm. (0.065-0.114 mm.), greatest body width average 0.097 mm. (0.075-0.147 mm.), average width of peduncle at junction with haptor 0.062 mm. (0.034-0.092 mm.). Haptor distinct, hexagonal in shape and broader than long, average width 0.107 mm. (0.076-0.127 mm.), average length 0.093 mm. (0.062-0.114 mm.). Ventral bar about size of dorsal bar, but straighter and with anterior surface raised in the midportion. Dorsal bar slightly bent ventrally in the middle and with obliquely truncate ends. Average length of ventral bar 0.036 mm. (0.029-0.038 mm.), average length of dorsal bar 0.036 mm. (0.030-0.040 mm.). Anchors similar in shape and size, bases bifurcate, superficial roots longer than deep roots. Wings clearly evident on all four anchor shafts. Anchors hollow distally, regularly recurved without formation of an angle at junction with points. Hollow portion of shaft continued into base of anchor point. Bases of dorsal and ventral anchors not markedly different in width. Average length of ventral anchors 0.032 mm. (0.026-0.034 mm.), average width 0.017 mm. (0.013-0.019 mm.), average length of dorsal anchors 0.032 mm. (0.026-0.036 mm.), average width 0.016 mm. (0.013-0.018 mm.). Hook bases ovate to elongate-ovate in shape. Hooks of pairs numbers one and five shorter than other hooks. The arrangement of the hooks is as described in the general morphology of the North American fresh-water *Tetraonchinae* possessing fourteen haptoral hooks (see pages 9, 15, and 62).

<i>Hook pair</i>	<i>Average length in mm.</i>	<i>Range in mm.</i>
1	0.015	0.011-0.017
2	0.019	0.015-0.021
3	0.020	0.015-0.023
4	0.021	0.015-0.023
5	0.015	0.010-0.017
6	0.021	0.015-0.023
7	0.020	0.015-0.023

Spatial relationships between members of the pairs of eye spots variable, anterior pair smaller.

Reproductive system.—Gonads situated anteriorly in the second half of body, testis ovate, slightly smaller than, and located dorsoposterior to ovary. Vas deferens arises from anterior end of testis, passes forward near midline of body and enters cirrus base without evident dilatation to form a seminal vesicle. Two prostate glands present, larger one irregularly saccate and filled with a finely granular fluid, smaller one elongate and containing a coarsely granular, yellowish fluid. Copulatory complex well developed and situated in a slender vestibule. Cirrus a long chitinous whip-like tube attenuated distally to a fine thread. Accessory piece a

chitinous structure with a deep groove which serves as cirrus guide. Muscular elements originate about midway on accessory piece and insert on base of cirrus. On contraction of these elements the portion of the accessory piece anterior to the attachment remains *in situ*, the portion of the accessory piece posterior to the attachment bends in elbow fashion and the cirrus is projected ventrally, through the vestibular pore, for a distance equal to about one-half its length.

Ovary ovate, slightly larger than testis and situated anteroventrally to it. Egg pore located on ventral surface on right of vestibular pore. Vagina present on left margin in anterior body half, vaginal canal a relatively long chitinous tube terminating at the well-developed seminal receptacle. Vitellaria and vitelline ducts are as described in the general morphology of the North American fresh-water Tetraonchinae. Shell gland not observed.

Digestive and excretory systems.—The digestive and excretory systems exist as described in the general morphology of the North American fresh-water Tetraonchinae. Average diameter of pharynx 0.034 mm. (0.030-0.048 mm.).

Systematic position.—This parasite, from Illinois localities, has been found to occur in mixed infestations with *Cleidodiscus vancleavei* Mizelle, 1936, *Cleidodiscus capax* Mizelle, 1936, and *Cleidodiscus longus* Mizelle, 1936. It has been recovered only from the gills of the white crappie. The vagina of this species is almost identical with that of *C. longus*. Whereas the shafts of *C. longus* are markedly dilated to form an internal angle at the junction with the points, the converse condition exists in the anchors of *C. uniformis*. The anchor shafts of *C. uniformis* are never more than slightly dilated, hollow and regularly recurved without formation of an angle at the locus mentioned above for *C. longus*. The ventral anchor bases of *C. longus* are much wider than are the dorsal anchor bases. The dorsal and ventral anchor bases of *C. uniformis* are almost identical in width. Average width of ventral anchor bases of *C. longus* 0.028 mm., average width of dorsal anchor bases 0.017 mm.; average width of ventral anchor bases of *C. uniformis* 0.017 mm., average width of dorsal anchor bases 0.016 mm. In addition to the above differences, the bars of the two species are constantly different in shape. *C. longus* is the nearest morphological relative of *C. uniformis*.

Forty-eight white crappies from Lake Decatur, Decatur, Ill., in May, June, July, and August, 1936, were one hundred per cent infested with this parasite. Only one host was taken from the Salt Fork of the Big Vermilion River south of Oakwood, Ill., July, 1936. Five hosts from Boomer Creek, Stillwater, Okla., were infested one hundred per cent with this species.

Cleidodiscus vancleavei Mizelle, 1936

Figs. 5, 31-39

Hosts and Localities: White and Black Crappies (*Pomoxis annularis* and *P. sparoides*), Lake Decatur, Decatur, Ill.; Salt Fork of the Big Vermilion River, south of Oakwood, Ill.; Boomer Creek, Stillwater, Okla.

Location: Gills.

Specimens: U.S.N.M. Helm. Coll. No. 9082.

Synonyms: *Onchocleidus formosus* Mueller, 1936; *C. formosus* (Mueller, 1936) Price, 1937.

General anatomy.—Relatively small parasites devoid of surface scales and internal spicules. Average length 0.563 mm. (0.399-0.681 mm.), average width at level of cephalic lobes 0.068 mm. (0.042-0.089 mm.), greatest body width average 0.070 mm. (0.057-0.089 mm.), average width of peduncle at junction with haptor 0.047 mm. (0.036-0.067 mm.). Haptor distinct, hexagonal in shape and broader than long, average width 0.104 mm. (0.089-0.124 mm.), average length 0.086 mm. (0.074-0.105 mm.). Dorsal bar notched at each end and with a median spine on the posterior border. Ends of ventral bar variable in shape, median posterior spine present. Average length of ventral bar 0.024 mm. (0.019-0.029 mm.), average length of dorsal bar 0.025 mm. (0.019-0.029 mm.). Anchors similar in shape, bases slightly bifurcate, superficial roots longer than deep roots, wings clearly evident. Each anchor shaft solid, junction with point marked by an internal angle. Ventral anchors slightly longer than dorsal anchors. Bases of dorsal and ventral anchors not noticeably different in width. Average length of ventral anchors 0.039 mm. (0.033-0.044 mm.), average width 0.019 mm. (0.013-0.023 mm.), average length of dorsal anchors 0.036 mm. (0.029-0.042 mm.), average width 0.017 mm. (0.015-0.019 mm.). Hook bases of pair number five ovate and shorter than shafts, bases of remaining hooks elongate. Bases of pair number one about same length as their shafts, bases of remaining hooks longer than their respective shafts. Hooks of pair number five noticeably shorter than the other hooks. The arrangement of the hooks is characteristic of North American Tetraonchinae possessing fourteen haptoral hooks (see pages 9, 15, and 62).

Hook pair	Average length in mm	Range in mm.
1	0.018	0.013-0.019
2	0.020	0.017-0.023
3	0.019	0.015-0.023
4	0.022	0.019-0.025
5	0.013	0.011-0.015
6	0.021	0.017-0.025
7	0.024	0.019-0.027

The anterior eye spots are smaller and farther apart than members of the posterior pair.

Reproductive system.—Gonads situated anteriorly in posterior body

half, testis relatively small and located posterior to ovary. Vas deferens dilated near cirrus base to form a tubular seminal vesicle. Two prostate glands, one containing a finely granular colorless fluid, the other filled with a coarsely granular faintly yellowish fluid. Copulatory complex well developed and situated in a small vestibule. Cirrus a short chitinous tube, base relatively large, shaft tapered to a point distally. Accessory piece a chitinous structure of variable shape. It encloses the base of the cirrus and usually makes one complete turn around the cirrus shaft. Operation of copulatory complex not observed.

Ovary ovate, much larger than testis and situated anterior to it. Egg pore on ventral surface anterior to base of copulatory complex. Vagina on left margin near midlength of body; vaginal canal short, emptying mesially into a transparent seminal receptacle. Vitellaria and vitelline ducts exist as described in the general morphology of the North American fresh-water Tetraonchinae. Nature of shell gland not determined.

Digestive and excretory systems.—The digestive and excretory systems are as given in the general morphology of the North American fresh-water Tetraonchinae. Average diameter of pharynx 0.025 mm. (0.023-0.028 mm.).

Systematic position.—This parasite, from Illinois localities, has been recovered from the gills of the white crappie, in mixed infestations with *Cleidodiscus capax* Mizelle, 1936, *Cleidodiscus longus* Mizelle, 1936, and *Cleidodiscus uniformis* Mizelle, 1936. It has been recovered from the gills of the black crappie in pure infestations. *C. capax* also occurs on the black crappie, but in this investigation these two parasites have not been recovered from the same host specimen. While the general morphology of *Cleidodiscus vancleavei* is similar to that of the rest of the members of the genus, the characteristic copulatory complex, together with the presence of spines on both the dorsal and ventral bars distinguish it immediately from all related forms. In May, June, July, and August, 1936, forty-eight white crappies from Lake Decatur, Decatur, Ill., were found one hundred per cent infested with this helminth. Only one host (white crappie) was taken from the Salt Fork of the Big Vermillion River. Six black crappies from Lake Decatur in June, 1936, were infested only fifty per cent with this parasite.

Mueller (1936a) described this parasite from the gills of the black crappie from Lake Okeechobee, Clewiston, Fla., as *Onchocleidus formosus*. The sinistral vagina and the copulatory complex with the accessory piece articulated to the cirrus base, definitely places this form in the genus *Cleidodiscus* Mueller, 1934. Mueller's specimens of *O. formosus* have been compared with specimens of *C. vancleavei*, and forms showing variation in the ventral bar and accessory piece identical

with Mueller's figures have been taken from the black and white crappies in Illinois and Oklahoma.

Cleidodiscus bedardi Mizelle, 1936

Figs. 6, 57-66

Host and Localities: Long-Eared Sunfish (*Xenotis megalotis*), Embarrass River, Urbana, Ill.

Location: Gills.

Specimens: U.S.N.M. Helm. Coll. No. 9083.

General anatomy.—Relatively small parasites devoid of surface scales and internal spicules. Average length 0.412 mm. (0.285-0.495 mm.), average width at level of cephalic lobes 0.056 mm. (0.047-0.067 mm.), greatest body width average 0.080 mm. (0.057-0.103 mm.), average width of peduncle at junction with haptor 0.057 mm. (0.038-0.065 mm.). Haptor distinct, subdiscoidal in shape and broader than long, average width 0.087 mm. (0.059-0.100 mm.), average length 0.058 mm. (0.051-0.067 mm.). Ventral bar noticeably larger than dorsal bar and variable in shape. Both bars bent near middle, dorsal bar always bent posteriorly, ventral bar may be bent either anteriorly or posteriorly. Average length of ventral bar 0.031 mm. (0.027-0.036 mm.), average length of dorsal bar 0.024 mm. (0.023-0.025 mm.). Anchors similar in shape, bases bifurcate, superficial roots slightly longer than deep roots. Anchor shafts solid, suggestion of internal angle at junction of shaft and point. Ventral anchor slightly longer than dorsal anchors. Ventral anchor bases not conspicuously wider than dorsal anchor bases. Average length of ventral anchors 0.027 mm. (0.023-0.034 mm.), average width 0.012 mm. (0.009-0.015 mm.), average length of dorsal anchors 0.024 mm. (0.021-0.032 mm.), average width 0.011 mm. (0.009-0.015 mm.). Hooks not conspicuously different in length. Bases of hooks ovate, bases of pair number five shorter than shafts, bases of other hooks about same length as their respective shafts. The arrangement of hooks is as described in the general morphology of the North American Tetraonchinae possessing fourteen haptor hooks (see pages 9, 15, and 62).

Hook pair	Average length in mm.	Range in mm.
1	0.013	0.011-0.015
2	0.014	0.011-0.015
3	0.014	0.013-0.015
4	0.014	0.013-0.015
5	0.012	0.009-0.013
6	0.015	0.013-0.016
7	0.014	0.013-0.015

Anterior eye spots smaller and generally farther apart than members of posterior pair.

Reproductive system.—Gonads located in posterior body half, testis ovate, situated dorsoposterior to and much smaller than ovary. Vas deferens passes forward generally on left side of body as a slightly undulant tube dilated near cirrus base to form a fusiform seminal vesicle. Only one prostate gland observed; it is saccate and contains a coarsely granular yellowish fluid. Copulatory complex well developed and situated in a relatively large vestibule. Cirrus a simple curved chitinous tube tapered distally to a fine point. Accessory piece a solid chitinous rod with a chelate termination. Operation of cirrus not observed.

Ovary subspherical, much larger than, and situated anteroventrally to the testis. Egg pore on ventral surface on right of copulatory complex. Vagina present on left margin near midlength of body; vaginal canal short, emptying into a small seminal receptacle lying parallel to the lateral margin of body. A pseudovagina (Fig. 64) occurs immediately anterior to the vagina. Vitellaria and vitelline ducts exist as described in the general morphology of the North American fresh-water Tetraonchinae. Shell gland a thickened portion of the oviduct.

Digestive and excretory systems.—The digestive and excretory systems are as described in the general morphology of the North American fresh-water Tetraonchinae. Average diameter of pharynx 0.025 mm. (0.021-0.032 mm.). A large solenocyte occurs in the region of the seminal receptacle.

Systematic position.—This parasite, from Illinois localities, occurs in mixed infestations with *Actinocleidus articularis* (Mizelle, 1936), *Onchocleidus distinctus* Mizelle, 1936, *Pterocleidus acuminatus* (Mizelle, 1936), an undescribed species of *Cleidodiscus* Mueller, 1934, and an undescribed member of the genus *Haplocleidus* Mueller, 1937. *Cleidodiscus bedardi* has been taken only from the gills of the long-eared sunfish from the Embarrass River south of Urbana, Ill. It is immediately recognizable by the striking difference in the size of the dorsal and ventral bars, the ventral being much larger; the presence of a pseudovagina; and a chelate accessory piece. The anchors are relatively small with deeply bifurcate bases. These structural details taken together are radically different from those of any other described member of the genus *Cleidodiscus*.

One hundred per cent infestation was recorded for one hundred twenty-five long-eared sunfish, from the Embarrass River in April, May, June, July, and August, 1936.

Cleidodiscus diversus sp. nov.

Figs. 141-147

Host and Localities: Green Sunfish (*Apomotis cyanellus*), Embarrass River, Urbana, Ill.; Boomer Creek, Stillwater, Okla.

Location: Gills.

Specimens: U.S.N.M. Helm. Coll. No. 9139.

General anatomy.—Relatively small parasites devoid of surface scales and internal spicules. Average length 0.340 mm. (0.205-0.394 mm.), greatest body width (near peduncle) average 0.061 mm. (0.052-0.085 mm.). Haptor distinct, hexagonal and broadly connected to peduncle. Ventral bar variable in shape, heavier and slightly longer than dorsal bar which is bent in middle to present a sagged appearance. Average length of ventral bar 0.029 mm. (0.025-0.034 mm.), average length of dorsal bar 0.021 mm. (0.019-0.023 mm.). Anchors similar in size and shape, bases bifurcate; wings on anchor shafts clearly discernible. Anchor points and shafts unite to form an internal angle at locus of junction. Average length of ventral anchors 0.025 mm. (0.021-0.032 mm.), average length of dorsal anchors 0.025 mm. (0.022-0.029 mm.). Each of the fourteen hooks is differentiated into a base, shaft, sickle-shaped termination, and opposable piece. Hook lengths 0.013-0.019 mm. Hook bases elongate-ovate and about same length as shafts. The arrangement of the hooks is characteristic of North American fresh-water Tetraonchinae possessing fourteen haptor hooks (see pages 9, 15, and 62). The anterior eye spots are smaller and generally farther apart than members of the posterior pair.

Reproductive system.—Gonads located anteriorly in posterior half of body; vas deferens arises from anterior end of testis, passes forward as a slightly undulant tube. Copulatory complex well developed and situated in a relatively large vestibule. Cirrus a short chitinous tube with a large base and tapered shaft, length 0.034 mm. (0.027-0.043 mm.). Accessory piece a doubly recurved chitinous structure with a knob near the midportion and with a forked termination. Operation of cirrus not observed.

Ovary ovate; egg pore located on ventral surface near vestibular pore. Vagina present on left margin near the middle of the body. The vitellaria and vitelline ducts are as described in the general morphology for the North American fresh-water Tetraonchinae. Shell gland not observed.

Digestive and excretory systems.—The digestive and excretory systems exist as described in the general morphology of the North American fresh-water Tetraonchinae. Average diameter of pharynx 0.021 mm. (0.017-0.027 mm.)

Systematic position.—*Cleidodiscus diversus* occurs in mixed infestations with *Cleidodiscus robustus* Mueller, 1934, *Onchocleidus cyanellus* n. sp., *Actinocleidus longus* n. sp., and an undescribed member of the genus *Actinocleidus* Mueller, 1937. *C. diversus* possesses anchors similar to those of *Cleidodiscus bedardi* Mizelle, 1936, and a copulatory complex like that of *Actinocleidus fergusonii*, n. sp. The former species occurs on

the long-eared sunfish, the latter on the bluegill, and *C. diversus* on the green sunfish. One hundred per cent infestation with this parasite is recorded for twenty-six green sunfish from the Embarrass River in May, 1937.

Genus *Onchocleidus* Mueller, 1936

Diagnosis.—Tetraonchinae with intestine bifurcate but confluent posteriorly. Vagina present or absent; when present it lies on the right body margin near the midlength. Copulatory complex weakly developed, cirrus a slender chitinous tube, at times with a fin or cirral thread around the shaft, at times corkscrew-like in nature. Accessory piece may be wanting but when present its base is not articulated with the cirrus base. Haptor generally distinct, hexagonal or pentagonal in shape. Fourteen hooks present, each of which may be solid and differentiated into a base, shaft, sickle-shaped termination and opposable piece, but generally exists as a solid or hollow cylindrical structure with a sickle-shaped termination and opposable piece distally. Parasitic on the gills of fresh-water fishes. Type species, *O. ferox* (Mueller, 1934).

Onchocleidus principalis Mizelle, 1936

Figs. 3, 76-84

Hosts and Localities: Kentucky Bass (*Micropterus pseudaplites*) and Small-Mouth Bass (*Micropterus dolomieu*), Salt Fork of the Big Vermilion River, Homer, Ill. Large-Mouth Bass (*Aplites salmoides*), Lake Senachwine, Henry, Ill.

Location: Gills.

Specimens: U.S.N.M. Helm. Coll. No. 9085.

Synonym: *Onchocleidus contortus* Mueller, 1937.

General anatomy.—Relatively small parasites devoid of body scales and internal spicules. Average length 0.467 mm. (0.369-0.631 mm.), average width at level of cephalic lobes 0.079 mm. (0.066-0.108 mm.), greatest body width average 0.096 mm. (0.070-0.127 mm.), average width of peduncle at junction with haptor 0.057 mm. (0.028-0.070 mm.). Haptor distinct, hexagonal in shape and broader than long, average width 0.098 mm. (0.078-0.125 mm.), average length 0.066 mm. (0.051-0.082 mm.). Ventral bar relatively straight and heavier than dorsal bar. Dorsal bar with midportion noticeably curved posteriorly, slightly shorter than ventral bar and with a notch on posterior margin near each end. Average length of ventral bar 0.036 mm. (0.032-0.042 mm.), average length of dorsal bar 0.035 mm. (0.030-0.044 mm.). Anchors similar in shape, wings slightly visible. Shaft and point of each anchor solid and relatively regularly recurved without formation of a distinct internal angle at their junction. Ventral anchors slightly longer than dorsal anchors. Average length of ventral anchors 0.033 mm. (0.028-0.038 mm.), average width 0.018 mm. (0.015-0.021 mm.), average length of dorsal anchors 0.031

mm. (0.027-0.034 mm.), average width 0.015 mm. (0.013-0.017 mm.). Bases of ventral anchors larger but not conspicuously wider than bases of the dorsal anchors. Each of the fourteen hooks differentiated into a base, shaft, sickle-shaped termination and opposable piece. Hook bases elongate, bases of pair number one about same length as their shafts, bases of pair number five shorter than their shafts, bases of remaining hooks slightly longer than their shafts. Hooks of pairs numbers one and five shorter than other hooks. The arrangement of the hooks is as described in the general morphology of the North American fresh-water *Tetraonchinae* possessing fourteen haptor hooks (see pages 9, 15, and 62).

<i>Hook pair</i>	<i>Average length in mm.</i>	<i>Range in mm.</i>
1	0.017	0.013-0.019
2	0.020	0.019-0.023
3	0.020	0.019-0.023
4	0.021	0.019-0.024
5	0.015	0.013-0.019
6	0.020	0.019-0.025
7	0.021	0.019-0.025

Anterior eye spots smaller and about the same distance apart as members of the posterior pair. In life, a refractile area is present immediately in front of each anterior eye spot.

Reproductive system.—Gonads located in posterior body half, testis ovate and situated dorsal to ovary. Vas deferens passes forward on left side of body and expands into a relatively large fusiform seminal vesicle just posterior to cirrus base. Two prostate glands present, larger one tubular and filled with a finely granular hyaline fluid, smaller gland an elongate bulb-like structure containing a coarsely granular yellowish fluid. Each prostate empties into base of cirrus by a single individual duct. Copulatory complex weakly developed and situated in a relatively small vestibule. Cirrus a chitinous corkscrew-like tube emptying ventrally through the vestibular pore. Accessory piece a solid chitinous structure about three-fifths the length of cirrus and with a forked termination which is often complete to form a ring through which the cirrus passes. Operation of cirrus not observed.

Ovary ovate and about two to three times as large as the testis. Egg pore located on the ventral surface at right of cirrus base. Vagina present on right margin about midway the body length; vaginal canal an undulant, lightly chitinized tube, often with one or two loose coils; seminal receptacle conspicuous. The vitellaria and vitelline ducts are as described in the general morphology of the North American fresh-water *Tetraonchinae*.

Digestive and excretory systems.—The digestive system agrees with

the description given for the North American fresh-water *Tetraonchinae*. Average diameter of the pharynx 0.029 mm. (0.025-0.034 mm.). Excretory system as described for the North American fresh-water *Tetraonchinae*, but an additional pair of ducts occur at level of seminal receptacle. One of these ducts is present on each side of the body and passes toward the lateral body margins. Openings for these structures have not been observed. Two very large solenocytes are present, one is located at the level of the ovary and the other near the posterior end of the seminal vesicle.

Systematic position.—This parasite is singular in that each of the fourteen hooks is differentiated into a base, shaft, sickle-shaped termination and opposable piece. While this character is common to the genus *Cleidodiscus* Mueller, 1934, the possession of other characters as vagina on right margin, and accessory piece not articulated to the cirrus base definitely places it in the genus *Onchocleidus* Mueller, 1936. The bars, anchors, vaginal tube, and hooks are distinctive.

Mueller (1937) described this parasite as *Onchocleidus contortus* from the large-mouth bass in Florida. The distal portion of the accessory piece of *O. principalis* was originally described (Mizelle, 1936) as forming a ring through which the cirrus projected. Mueller (1937) distinguished *O. contortus* from *O. principalis* by the forked termination of the accessory piece. This structural variation of the accessory piece was earlier recognized by the present author. Specimens of these two species have been compared and found to be identical. Hosts, for this species, have been found one hundred per cent infested.

Onchocleidus interruptus Mizelle, 1936

Figs. 2, 103-108

Host and Localities: Yellow Bass (*Morone interrupta*), Lake Decatur, Decatur, Ill.; Lake Senachwine, Henry, Ill.

Location: Gills.

Specimens: U.S.N.M. Helm. Coll. No. 9088.

General anatomy.—Relatively small parasites devoid of surface scales and internal spicules. Average length 0.407 mm. (0.285-0.508 mm.), average width at level of cephalic lobes 0.073 mm. (0.067-0.080 mm.), greatest body width average 0.085 mm. (0.066-0.104 mm.), average width of peduncle at junction with haptor 0.057 mm. (0.046-0.070 mm.). Haptor distinct, hexagonal in shape and broader than long, average width 0.097 mm. (0.086-0.133 mm.), average length 0.078 mm. (0.066-0.095 mm.). Ventral bar slightly longer than dorsal bar and with a cavity in its posterior midportion. Both bars slightly bent in the middle. Average length of ventral bar 0.033 mm. (0.029-0.044 mm.), average length of

dorsal bar 0.030 mm. (0.027-0.036 mm.). Anchors similar in shape, bases bifurcate superficial roots longer than deep roots. Anchor wings clearly perceptible. Each anchor shaft solid and uniting with its point to form an internal angle at junction. Ventral anchors longer than dorsal anchors. Average length of ventral anchors 0.045 mm. (0.040-0.052 mm.), average width 0.024 mm. (0.019-0.032 mm.), average length of dorsal anchors 0.040 mm. (0.036-0.050 mm.), average width 0.014 mm. (0.013-0.021 mm.). Bases of ventral anchors noticeably wider than bases of dorsal anchors. Each hook, except pair number five, consists of an elongate chitinous body with an opposable piece and sickle-shaped termination. Each hook of pair number five is differentiated into a base, shaft, sickle-shaped termination, and opposable piece. Hooks of pair number one longer, and hooks of pair number five conspicuously shorter than rest of hooks. The arrangement of hooks is as given in the general morphology of the North American fresh-water Tetraonchinae possessing fourteen haptoral hooks (see pages 9, 15, and 62).

<i>Hook pair</i>	<i>Average length in mm.</i>	<i>Range in mm.</i>
1	0.032	0.028-0.040
2	0.024	0.021-0.025
3	0.024	0.021-0.027
4	0.023	0.019-0.032
5	0.013	0.011-0.015
6	0.026	0.021-0.032
7	0.029	0.027-0.034

The spatial relationships between members of the two pairs of eye spots variable, anterior pair smaller.

Reproductive system.—Gonads situated anteriorly in the posterior body half, testis ovate, from four to six times as large as ovary and located posterior to it. Vas deferens dilated immediately posterior to cirrus base to form a conspicuous seminal vesicle. Two prostate glands present, large one saccate, filled with a finely granular, colorless fluid, smaller one botuliform and containing a coarsely granular yellowish fluid. Copulatory complex weakly developed and enclosed within a slender vestibule. Cirrus a short, straight, chitinous tube attenuated distally, expanded terminally, and with a cirral thread around the shaft. Accessory piece solid, with a key-hole effect distally through which one of the loops of the cirral thread passes. Operation of copulatory complex not fully understood.

Ovary subspherical, much smaller than testis and situated anterior to it. Egg pore on ventral surface on right of copulatory complex. Vagina and seminal receptacle wanting in this species. Vitellaria and vitelline ducts are as described in the general morphology of the North American fresh-water Tetraonchinae. Shell gland not observed.

Digestive and excretory systems.—The digestive and excretory systems are as described in the general morphology of the North American fresh-water Tetraonchinae. Average diameter of pharynx 0.028 mm. (0.023-0.032 mm.).

Systematic position.—This parasite has been collected only from the gills of the yellow bass. It is the only monogenetic form recorded from this host. *Onchocleidus interruptus* is easily recognized by the massive testis and the characteristic bars and anchors. The shafts of the ventral anchors are noticeably bent in the direction of the points. The copulatory complex resembles that of *Onchocleidus distinctus* Mizelle, 1936, a form which occurs on the long-eared sunfish. Sixty-five hosts from Lake Decatur in May, June, July, and August, 1936, and eight hosts from Lake Senachwine in June, 1936, were infested one hundred per cent with *O. interruptus*.

Onchocleidus mucronatus Mizelle, 1936

Figs. 9, 22-30

Hosts and Localities: Bluegill Sunfish (*Helioperca macrochira*), Orange-spotted Sunfish (*Allotis humilis*), Pumpkinseed Sunfish (*Eupomotis gibbosus*), Hybrid between Bluegill and Pumpkinseed Sunfishes and Hybrid between Orange-spotted and Pumpkinseed Sunfishes, Lake Senachwine, Henry, Ill.—Bluegill Sunfish, Lake Decatur, Decatur, Ill.; Boomer Creek, Stillwater, Okla.—Orange-spotted Sunfish, Salt Fork of the Big Vermilion River, Homer, Ill.

Location: Gills.

Specimens: U.S.N.M. Helm. Coll. No. 9087.

General anatomy.—Relatively small parasites devoid of surface scales and internal spicules. Average length 0.503 mm. (0.426-0.820 mm.), average width at level of cephalic lobes 0.051 mm. (0.041-0.098 mm.), greatest body width average 0.065 mm. (0.051-0.131 mm.), average width of peduncle at junction with haptor 0.042 mm. (0.019-0.075 mm.). Haptor distinct, hexagonal or pentagonal in shape and broader than long, average width 0.101 mm. (0.070-0.148 mm.), average length 0.098 mm. (0.076-0.139 mm.). Each bar possesses a spine projecting from middle of posterior margin. Average length of ventral bar 0.022 mm. (0.019-0.024 mm.), average length of dorsal bar 0.024 mm. (0.021-0.025 mm.). Wings on anchor shafts delicate. Anchors similar in shape, bases slightly bifurcate, superficial roots longer than deep roots. Anchor shafts solid and unite with anchor points to form an internal angle at junction. Anchors approximately same size. Average length of ventral anchors 0.057 mm. (0.051-0.067 mm.), average width 0.014 mm. (0.009-0.019 mm.), average length of dorsal anchors 0.057 mm. (0.051-0.074 mm.), average width 0.012 mm. (0.009-0.019 mm.). Each hook, except pair number five, has an elongate chitinous body, a sickle-shaped termination, and opposable piece. Each hook of pair number five possesses a base,

shaft, sickle-shaped termination and opposable piece. Hooks of pairs numbers one and seven with apparent cavity, members of pair number two often with slight cavity. Hooks of pair number one noticeably longer and hooks of pair number five conspicuously shorter than other hooks. The arrangement of the hooks is as given in the general morphology of the North American fresh-water Tetraonchinae possessing fourteen haptor al hooks (see pages 9, 15, and 62).

<i>Hook pair</i>	<i>Average length in mm.</i>	<i>Range in mm.</i>
1	0.035	0.030-0.043
2	0.026	0.023-0.032
3	0.030	0.025-0.037
4	0.032	0.028-0.038
5	0.013	0.010-0.015
6	0.033	0.028-0.038
7	0.031	0.028-0.044

Anterior eye spots smaller and usually farther apart than members of the posterior pair.

Reproductive system.—Gonads located in posterior half of body, testis subspherical, located posterior to, and from two to three times as large as ovary. Vas deferens passes forward generally making one loop in front of vaginal canal and dilates posterior to cirrus base to form an elongate seminal vesicle. Two prostate glands present, larger one banana-shaped, containing a finely granular colorless fluid, smaller one saccate and filled with a coarsely granular yellowish fluid. Each prostate gland empties into cirrus base by a single individual duct. Copulatory complex weakly developed and enclosed within a slender vestibule. Cirrus a chitinous tube with a cirral thread around the shaft. Accessory piece a solid chitinous structure with a key-hole effect distally through which the cirrus projects. Muscular elements arise on accessory piece and insert on base of cirrus; on contraction of these elements the accessory piece remains *in situ*, and the cirrus is projected ventrally, through the vestibular pore, a short distance beyond the body surface. Retraction of cirrus not fully understood.

Ovary subspherical, about one-third to one-half the size of testis and situated anterior to it. Egg pore on ventral surface near vestibular pore. Vagina on right body margin near midlength; vaginal canal a short zigzag, chitinous tube emptying into a small bag-like seminal receptacle. Vitellaria and vitelline ducts as described in the general morphology of the North American fresh-water Tetraonchinae. Shell gland a cluster of cells surrounding the ootype.

Digestive and excretory systems.—Digestive and excretory systems as given in the general morphology of the North American fresh-water

Tetraonchinae. Average diameter of pharynx 0.027 mm. (0.024-0.039 mm.).

Systematic position.—This species occurs in mixed infestations with *Cleidodiscus robustus* Mueller, 1934, *Haploclaidus dispar* (Mueller, 1936), *Pterocleidus acer* (Mueller, 1936) and *Actinocleidus fergusoni* n. sp. on the bluegill sunfish. Superficially the copulatory complex is similar to that of *H. dispar*. Each bar of *O. mucronatus* possesses a spine on the posterior middle region, a condition seldom found in the genus. Specimens of *O. mucronatus* from Lake Senachwine were almost twice the size of those from the same host, viz., the bluegill sunfish, from Lake Decatur. One hundred per cent infestation with this parasite is recorded for: nineteen bluegills from Lake Chautauqua, Havana, Ill., in May, 1936; five hybrids between the bluegill and pumpkinseed sunfishes from Lake Senachwine, Henry, Ill., in June, 1936; six hybrids between the orange-spotted and pumpkinseed sunfishes from Lake Senachwine, Henry, Ill., in June, 1936; four orange-spotted sunfish from the Salt Fork of the Big Vermilion River, Homer, Ill., in April, 1936; and one bluegill sunfish from the Illinois State Natural History Survey pond, Urbana, Ill., in July, 1936. Twelve bluegills from Lake Senachwine in June, 1936, were infested seventy-five per cent.

Onchocleidus distinctus Mizelle, 1936

Figs. 8, 109-117

Host and Locality: Long-eared Sunfish (*Xenotis megalotis*), Embarrass River, Urbana, Ill.

Location: Gills.

Specimens: U.S.N.M. Helm. Coll. No. 9086.

General anatomy.—Relatively small parasites devoid of body scales and internal spicules. Average length 0.476 mm. (0.344-0.590 mm.), average width at level of cephalic lobes 0.065 mm. (0.048-0.072 mm.), greatest body width average 0.070 mm. (0.050-0.095 mm.), average width of peduncle at junction with haptor 0.046 mm. (0.032-0.057 mm.). Haptor distinct, hexagonal or pentagonal in shape and broader than long, average width 0.078 mm. (0.064-0.110 mm.), average length 0.070 mm. (0.057-0.086 mm.). Ventral bar slightly shorter than dorsal bar. Average length of ventral bar 0.024 mm. (0.021-0.027 mm.), average length of dorsal bar 0.026 mm. (0.023-0.029 mm.). Anchors similar in shape, bases slightly bifurcate, superficial roots longer than deep roots. Anchor wings weakly developed. Distal portion of each anchor shaft slightly dilated and hollow. Internal angle at junction of each anchor shaft and point. Ventral anchors slightly longer than dorsal anchors. Average length of ventral anchors 0.035 mm. (0.032-0.038 mm.), average width

0.016 mm. (0.013-0.019 mm.), average length of dorsal anchors, 0.034 mm. (0.030-0.036 mm.), average width 0.013 mm. (0.011-0.015 mm.). Bases of ventral anchors not conspicuously wider than bases of the dorsal anchors. Each of the fourteen hooks consists of an elongate cylindrical body with a sickle-shaped termination and opposable piece distally. Body of each hook of pair number five, which lies between the shafts of ventral anchors, shows a tendency toward differentiation into a base and shaft. Hooks of pairs numbers one, six, and seven possess hollow bodies, hooks of pair number two often have slightly hollow bodies, rest of hook bodies solid. Hooks of pair number one larger and hooks of pair number five conspicuously smaller than rest of hooks. The arrangement of the hooks is as given in the general morphology of the North American fresh-water Tetraonchinae possessing fourteen haptor al hooks (see pages 9, 15, and 62).

<i>Hook pair</i>	<i>Average length in mm.</i>	<i>Range in mm.</i>
1	0.032	0.027-0.036
2	0.026	0.023-0.030
3	0.026	0.023-0.029
4	0.028	0.023-0.030
5	0.010	0.009-0.012
6	0.029	0.025-0.032
7	0.030	0.027-0.034

Anterior eye spots smaller and almost invariably farther apart than members of posterior pair.

Reproductive system.—Gonads located anteriorly in the posterior body half, testis ovate, smaller than ovary and situated posterior to it. The vas deferens arises from anterior end of testis, passes forward on left side of body and expands into a fusiform seminal vesicle near cirrus base. Two prostate glands present, each tubular in shape, smaller one about three-fourths the size of larger, and filled with a finely granular colorless fluid, larger one containing a coarsely granular yellowish fluid. Copulatory complex weakly developed and situated in a relatively small vestibule. Cirrus a small chitinous tube with a cirral thread around the shaft. Accessory piece a partial sleeve, open proximally and complete distally, and enclosing cirrus. Contractile elements arise on inner surface of accessory piece and insert on base of cirrus. On contraction of these structures the accessory piece remains *in situ*, and the cirrus is projected ventrally through the vestibular pore, for a short distance beyond the body surface. Retraction of the cirrus not understood.

Ovary ovate, larger than testis and situated anterior to it. Egg pore on ventral surface near vestibular pore. Vagina on right margin near termination of first body half; vaginal canal a chitinized tube emptying

mesially into a small seminal receptacle. Vitellaria and vitelline ducts are as described in the general morphology of the North American fresh-water Tetraonchinae. Shell gland not observed.

Digestive and excretory systems.—The digestive system is as described in the general morphology of the North American fresh-water Tetraonchinae. Average diameter of pharynx 0.023 mm. (0.019-0.028 mm.). The excretory system is common to the North American fresh-water Tetraonchinae. Two especially large solenocytes are present immediately anterior to the level of the ovary; a third flame cell is present in the region of the seminal receptacle.

Systematic position.—This parasite occurs in mixed infestations with *Cleidodiscus bedardi* Mizelle, 1936, *Actinocleidus articularis* (Mizelle, 1936), *Pterocleidus acuminatus* (Mizelle, 1936), an undescribed species of the genus *Cleidodiscus* Mueller, 1934, and an undescribed species of *Haplocleidus* Mueller, 1937. It has been recovered only from the long-eared sunfish. The cirrus superficially resembles the cirrus of *Onchocleidus mimus* Mueller, 1936. The accessory piece is wanting in *O. mimus* but is present in *Onchocleidus distinctus*. The vaginal canal, bars, and slightly dilated and hollow anchors, are conspicuously different from any other described member of the genus. One hundred per cent infestation is recorded for one hundred twenty-five hosts taken from the Embarrass River during the months of April, May, June, July, and August, 1936.

Onchocleidus cyanellus sp. nov.

Figs. 135-140

Host and Locality: Green Sunfish (*Apomotis cyanellus*), Embarrass River, Urbana, Ill.

Location: Gills.

Specimens: U.S.N.M. Helm. Coll. No. 9142.

General anatomy.—Relatively small parasites devoid of surface scales and internal spicules. Average length 0.572 mm. (0.328-0.738 mm.), greatest body width average 0.096 mm. (0.067-0.114 mm.). Haptor distinct, hexagonal in shape and broader than long. Each bar possesses a spine projecting from middle of posterior margin. Average length of ventral bar 0.024 mm. (0.021-0.027 mm.), average length of dorsal bar 0.025 mm. (0.021-0.029 mm.). Wings on anchor shafts delicate. Anchors similar in shape, bases slightly bifurcate, superficial roots noticeably longer than deep roots. Anchor shafts solid and unite with anchor points to form an internal angle at junction. Anchors approximately same size. Average length of ventral anchors 0.052 mm. (0.048-0.057 mm.), average length of dorsal anchors 0.053 mm. (0.049-0.059). Each hook has an elongate chitinous body with a sickle-shaped termi-

nation and opposable piece distally. Hooks of pair number five show a tendency toward differentiation into a base, shaft, sickle-shaped termination and opposable piece. Length of hooks of pair number five 0.008-0.013 mm., length of rest of hooks 0.024-0.032 mm. The arrangement of the hooks is as given in the general morphology of the North American fresh-water Tetraonchinae possessing fourteen haptor al hooks (see pages 9, 15, and 62). Anterior eye spots smaller and usually farther apart than members of the posterior pair.

Reproductive system.—Gonads located in posterior half of body; vas deferens passes forward as a slightly undulant tube. Copulatory complex weakly developed and enclosed within a slender vestibule. Cirrus a chitinous tube with a cirral thread around the shaft, length 0.035 mm. (0.032-0.040 mm.); accessory piece vestigial. Operation of cirrus not observed.

Ovary subspherical; egg pore on ventral surface near vestibular pore. Vagina on right body margin near midlength. Vitellaria and vitelline ducts as described in the general morphology of the North American fresh-water Tetraonchinae. Shell gland not observed.

Digestive and excretory systems.—Digestive and excretory systems are as given in the general morphology of the North American fresh-water Tetraonchinae. Average diameter of pharynx 0.024 mm. (0.018-0.036 mm.).

Systematic position.—This species occurs in mixed infestations with *Cleidodiscus diversus* n. sp., *Cleidodiscus robustus* Mueller, 1934, *Actinocleidus longus* n. sp., and an undescribed member of the genus *Actinocleidus* Mueller, 1937. The anchors and bars resemble those of *Onchocleidus mucronatus* Mizelle, 1936. The copulatory complex is different from the foregoing species and the zigzag vaginal tube characteristic of *O. mucronatus* is wanting. One hundred per cent infestation is recorded for twenty-six green sunfish from the Embarrass River in May, 1937.

Genus *Actinocleidus* Mueller, 1937

Diagnosis.—Tetraonchinae with intestine bifurcate but confluent posteriorly. Vagina present on left body margin near the midlength. Copulatory complex consisting of a cirrus and accessory piece. Accessory piece well developed, always present, and articulated to the cirrus base. Haptor distinct, discoidal in shape, and has both pairs of anchors on the ventral surface. The bars connecting the anchor bases are articulated with each other in their midregions. Each of the fourteen hooks present is differentiated into a base, shaft, sickle-shaped termination and opposable piece. Parasitic on the gills of fresh-water fishes. Type species, *Actinocleidus oculatus* (Mueller, 1934).

Actinocleidus articularis (Mizelle, 1936)

Figs. 10, 40-48

Host and Locality: Long-eared Sunfish (*Xenotis megalotis*), Embarrass River, Urbana, Illinois.

Location: Gills.

Specimen: U.S.N.M. Helm. Coll. No. 9084.

General anatomy.—Relatively small gill parasites with internal spicules and surface scales wanting. Average length 0.470 mm. (0.360-0.615 mm.), average width at level of cephalic lobes 0.062 mm. (0.049-0.082 mm.), greatest body width average 0.068 mm. (0.049-0.079 mm.), average width of peduncle at junction with haptor 0.041 mm. (0.028-0.067 mm.). Haptor distinct, disc-like in shape and broader than long, average width 0.072 mm. (0.061-0.086 mm.), average length 0.055 mm. (0.047-0.057 mm.). Anterior bar noticeably bent posteriorly in mid-portion with a notch present near each end on posterior margin. Posterior bar modified to form a plate-like structure, anterior end of which articulates with posterior surface of anterior bar. Average length of anterior bar 0.037 mm. (0.032-0.042 mm.), average length of posterior bar 0.022 mm. (0.019-0.025 mm.). Anchors similar in shape and size, bases nonbifurcate, deep roots vestigial. Anchor wings moderately developed. Anchor shafts solid and regularly recurved without formation of an angle at junction with hollow points. Average length of anterior anchors 0.033 mm. (0.032-0.038 mm.), average width 0.010 mm. (0.009-0.013 mm.), average length of posterior anchors 0.032 mm. (0.028-0.038 mm.), average width 0.010 mm. (0.008-0.011 mm.). Bases of hooks sub-spherical in shape and very short as compared with shafts. Hooks of pair number one slightly shorter than rest of hooks. Arrangement of the hooks is as described in the general morphology of the North American fresh-water Tetraonchinae with fourteen haptoral hooks (See pages 9, 15, and 62).

Hook pair	Average length in mm.	Range in mm
1	0.011	0.009-0.015
2	0.014	0.013-0.015
3	0.015	0.013-0.019
4	0.015	0.013-0.017
5	0.014	0.013-0.015
6	0.015	0.013-0.019
7	0.014	0.013-0.015

Anterior eye spots smaller and usually farther apart than members of the posterior pair.

Reproductive system.—Gonads situated in posterior half of body, testis ovate, about same size as ovary and located dorsoposterior to it.

Vas deferens arises from anterior end of testis and passes forward as an undulant tube and dilates slightly to form a tubular seminal vesicle near cirrus base. Two prostate glands present, smaller one somewhat bulbular in shape and filled with a finely granular colorless fluid, larger one bulbular in shape and containing a coarsely granular yellowish fluid. Copulatory complex well developed and situated in a moderate-sized vestibule. Cirrus a chitinous tube with a large base and a doubly recurved shaft which ends in a forked termination. Accessory piece a chitinous structure of an aviform shape. Operation of copulatory complex not observed.

Ovary ovate in outline, about same size as testis and located antero-ventrally to it. Egg pore located on ventral surface on right of copulatory complex. Vagina present on left margin near midlength of body; vaginal canal a short chitinous tube emptying into a transparent seminal receptacle which lies at anterior end of ovary. Vitellaria and vitelline ducts as described in the general morphology of North American fresh-water Tetraonchinae. Shell gland not observed.

Digestive and excretory systems.—Digestive and excretory systems as given in the general morphology of the North American fresh-water Tetraonchinae. Average diameter of pharynx 0.025 mm. (0.021-0.028 mm.).

Systematic position.—This species, from Illinois localities, occurs in mixed infestations with *Onchocleidus distinctus* Mizelle, 1936, *Cleidodiscus bedardi* Mizelle, 1936, *Pterocleidus acuminatus* (Mizelle, 1936), an undescribed species of *Cleidodiscus* Mueller, 1934, and an undescribed species of the genus *Haploleidus* Mueller, 1937. *Actinocleidus oculatus* (Mueller, 1934), structurally stands closer to this species than does any other member of the genus. *Actinocleidus articularis* is readily distinguishable from *A. oculatus* by the presence of hollow anchor points, a doubly recurved cirrus, and an aviform accessory piece. The former species has been taken only from the long-eared sunfish, whereas the latter is common only to the pumpkinseed sunfish (*Eupomotis gibbosus*). One hundred twenty-five long-eared sunfish taken from the Embarrass River south of Urbana, Ill., in the months of April, May, June, July, and August, 1936, were infested one hundred per cent with this parasite.

Actinocleidus longus sp. nov.

Figs. 166-172

Host and Localities: Green Sunfish (*Apomotis cyanellus*), Embarrass River, Urbana, Ill.; Boomer Creek, Stillwater, Okla.

Location: Gills.

Specimen: U.S.N.M. Helm. Coll. No. 9140.

General anatomy.—Relatively small gill parasites with internal spicules and surface scales wanting. Average length 0.444 mm. (0.336-0.573 mm.), greatest body width average 0.069 mm. (0.055-0.095 mm.). Haptor distinct, disc-like in shape and broader than long. Anterior bar noticeably bent posteriorly in midportion, and articulated with central portion of posterior bar. Average length of anterior bar 0.044 mm. (0.036-0.049 mm.), average length of posterior bar 0.031 mm. (0.027-0.040 mm.). Anchors similar in shape and size, bases nonbifurcate, deep roots vestigial. Anchor wings well developed. Anchor shafts hollow and regularly recurved without formation of an angle at junction with hollow points. Average length of anterior anchors 0.036 mm. (0.034-0.038 mm.), average length of posterior anchors 0.037 mm. (0.032-0.042 mm.). Bases of hooks subspherical in shape and very short as compared with shafts, hook lengths 0.013-0.017 mm. Arrangement of the hooks is as described in the general morphology of the North American fresh-water Tetraonchinae with fourteen haptor hooks (see pages 9, 15, and 62). Anterior eye spots smaller and usually farther apart than members of the posterior pair.

Reproductive system.—Gonads situated in posterior half of body; vas deferens arises from anterior end of testis and passes forward as an undulant tube. Copulatory complex well developed and situated in a moderate-sized vestibule. Cirrus a chitinous tube with a moderately large base, and attenuated to form a hair-like tube in the middle, but moderately enlarged distally. Accessory piece whip-like and much shorter than the cirrus. Operation of copulatory complex not observed.

Ovary ovate in outline; egg pore located on ventral surface near vestibular pore. Vagina present on left margin near midlength of body. Vitellaria and vitelline ducts as described in the general morphology of North American fresh-water Tetraonchinae. Shell gland not observed.

Digestive and excretory systems.—Digestive and excretory systems as given in the general morphology of the North American fresh-water Tetraonchinae. Average diameter of pharynx 0.026 mm. (0.021-0.029 mm.).

Systematic position.—This species occurs in mixed infestations with *Cleidodiscus diversus* n. sp., *Cleidodiscus robustus* Mueller, 1934, *Onchocleidus cyanellus* n. sp., and an undescribed species of *Actinocleidus* Mueller, 1937. This species has been collected only from the green sunfish. It possesses a copulatory complex somewhat similar to that of *Cleidodiscus longus* Mizelle, 1936, from the white crappie, and anchors, hooks, and bars resembling those of *Actinocleidus articularis* (Mizelle, 1936). One hundred per cent infestation with this parasite is recorded for twenty-six green sunfish from the Embarrass River in May, 1937.

Actinocleidus fergusonii sp. nov.

Figs. 148-153

Host and Localities: Bluegill Sunfish (*Helioperca macrochira*), Lake Senachwine, Henry, Ill.; Boomer Creek, Stillwater, Okla.

Location: Gills.

Specimens: U.S.N.M. Helm. Coll. No. 9141.

General anatomy.—Relatively small parasites devoid of surface scales and internal spicules. Average length 0.379 mm. (0.330-0.444 mm.), greatest body width average 0.056 mm. (0.045-0.083 mm.). Haptor distinct, subdiscoidal in shape and broader than long. Anterior bar bent posteriorly in the middle; posterior bar modified to articulate with anterior bar. Average length of anterior bar 0.029 mm. (0.025-0.033 mm.), average length of posterior bar 0.019 mm. (0.012-0.025 mm.). Anchors similar in shape, nonbifurcate, superficial roots elongate, deep roots vestigial. Anchor shafts hollow and regularly recurved without formation of angle at junction with hollow points. Anchors similar in size and shape. Average length of anterior anchors 0.025 mm. (0.023-0.027 mm.), average length of posterior anchors 0.023 mm. (0.021-0.025 mm.). Hooks not conspicuously different in length. Hook lengths 0.009-0.015 mm. Hook bases subspherical and much shorter than hook shafts. The arrangement of hooks as described in the general morphology of the North American fresh-water Tetraonchinae possessing fourteen haptor al hooks (see pages 9, 15, and 62). Anterior eye spots smaller and generally farther apart than members of the posterior pair.

Reproductive system.—Gonads located in posterior body half, testis ovate, situated dorsoposterior to and about same size as ovary. Vas deferens passes forward as a slightly undulant tube. Copulatory complex well developed and situated in a moderately large vestibule. Cirrus a simple curved chitinous tube with large base, and tapered distally to a fine point, average length 0.023 mm. (0.021-0.028 mm.). Accessory piece with two curves and with a knob near the middle. Operation of cirrus not observed.

Ovary subspherical, and situated anteroventrally to testis. Egg pore on ventral surface on right of copulatory complex. Vagina present on left margin near midlength of body. Vitellaria and vitelline ducts exist as described in the general morphology of the North American fresh-water Tetraonchinae. Shell gland not observed.

Digestive and excretory systems.—The digestive and excretory systems are as described in the general morphology of the North American fresh-water Tetraonchinae. Average diameter of pharynx 0.017 mm. (0.012-0.025 mm.).

Systematic position.—This parasite, from Illinois localities, occurs in

mixed infestations with *Cleidodiscus robustus* Mueller, 1934, *Onchocleidus mucronatus* Mizelle, 1936, *Pterocleidus acer* (Mueller, 1936) and *Haplocleidus dispar* (Mueller, 1936). This species is closely related to *Actinocleidus gracilis* Mueller, 1937. The cirrus of *Actinocleidus fergusonii* is sickle-shaped whereas the cirrus of *A. gracilis* is an undulant tube. Only slight infestation of the bluegill sunfish is recorded for this parasite.

Genus *Pterocleidus* Mueller, 1937

Diagnosis.—Tetraonchinae with intestine bifurcate but confluent posteriorly. The vagina, when present, is located on the right body margin near the midlength. Copulatory complex consisting of a cirrus, cirral thread, and accessory piece or a cirrus and cirral fin. The accessory piece, when present is never articulated with the cirrus base. Haptor distinct, pentagonal or hexagonal in shape. Each anchor shaft possesses a spur-like projection near the origin of the anchor point. The bars connecting the anchor bases are not articulated with each other. Each haptoral hook generally consists of a solid or hollow shaft terminating distally in a sickle-shaped structure and opposable piece. Parasitic on the gills of fresh-water fishes. Type species *Pterocleidus acer* (Mueller, 1936).

Pterocleidus acuminatus (Mizelle, 1936)

Figs. 11, 94-102

Host and Locality: Long-Eared Sunfish (*Xenotis megalotis*), Embarrass River, Urbana, Ill.

Location: Gills.

Specimens: U.S.N.M. Helm. Coll. No. 9089.

General anatomy.—Relatively small parasites devoid of surface scales and internal spicules. Average length 0.495 mm. (0.338-0.640 mm.), average width at level of cephalic lobes 0.066 mm. (0.052-0.095 mm.), greatest body width average 0.093 mm. (0.066-0.118 mm.), average width of peduncle at junction with haptor 0.053 mm. (0.038-0.068 mm.). Haptor distinct, hexagonal or pentagonal in shape and slightly broader than long, average width 0.078 mm. (0.064-0.104 mm.), average length 0.077 mm. (0.068-0.098 mm.). Ventral bar smaller than dorsal bar, both bars with a gentle posterior slope in the midregions. Average length of ventral bar 0.025 mm. (0.019-0.027 mm.), average length of dorsal bar 0.026 mm. (0.022-0.029 mm.). Anchors similar in size and shape, bases slightly bifurcate, superficial roots longer than deep roots. Anchor shafts solid, junction with points forms an internal angle. Spurs on anchor shafts well developed. Anchor wings clearly discernible. Average length of ventral anchors 0.047 mm. (0.040-0.051 mm.), average width 0.014 mm. (0.011-0.017 mm.), average length of dorsal anchors 0.048 mm.

(0.040-0.053 mm.), average width 0.013 mm. (0.010-0.017 mm.). Each hook consists of an elongate, solid chitinous body with a sickle-shaped termination and opposable piece distally. Hooks of pairs numbers one, six, and seven larger and pair number five noticeably smaller than rest of hooks. The arrangement of the hooks is as given in the general morphology of the North American fresh-water Tetraonchinae possessing fourteen haptoral hooks (see pages 9, 15, and 62).

<i>Hook pair</i>	<i>Average length in mm.</i>	<i>Range in mm.</i>
1	0.026	0.021-0.029
2	0.020	0.015-0.023
3	0.022	0.015-0.025
4	0.025	0.019-0.029
5	0.012	0.009-0.015
6	0.026	0.020-0.029
7	0.027	0.023-0.029

Anterior eye spots smaller and almost invariably farther apart than members of the posterior pair.

Reproductive system.—Gonads located anteriorly in posterior body half, testis ovate, posterior to, and about same size as ovary. Vas deferens passes forward on left side of body and dilates to produce a spindle-shaped seminal vesicle immediately posterior to cirrus base. Two prostate glands present, banana-shaped, and about of equal size. One of the prostate glands contains a finely granular colorless hyaline fluid, the other contains a coarsely granular yellowish fluid. Each prostate gland empties into cirrus base by a single individual duct. Copulatory complex weakly developed and enclosed within a slender vestibule. Cirrus a corkscrew-like chitinous tube with a moderate-sized base. Accessory piece a ploughshare-shaped structure lying along side of cirrus proximally and complete distally to form a ring through which the cirrus passes. Operation of cirrus not observed.

Ovary ovate, about size of testis and situated anterior to it. Egg pore located on ventral surface near vestibular pore. Vagina present on right body margin near midlength; vaginal canal a chitinized tube often making one or two loops before emptying mesially into the seminal receptacle. Vitellaria and vitelline ducts as described in the general morphology of the North American fresh-water Tetraonchinae. Shell gland not observed.

Digestive and excretory systems.—The digestive and excretory systems exist as described for the North American fresh-water Tetraonchinae. Average diameter of pharynx 0.026 mm. (0.019-0.030 mm.). Two large flame cells present, one at level of seminal receptacle, the other one at level of copulatory complex.

Systematic position.—This species occurs in mixed infestations with *Cleidodiscus bedardi* Mizelle, 1936, *Actinocleidus articularis* (Mizelle, 1936), *Onchocleidus distinctus* Mizelle, 1936, and an undescribed member of *Haplocleidus* Mueller, 1937, and undescribed member of *Cleidodiscus* Mueller, 1934. The cirrus of *Pterocleidus acuminatus* resembles that of *Onchocleidus principalis* Mizelle, 1936, but the anchors possess spur-like structures which are characteristic of the genus *Pterocleidus*. *P. acuminatus* has been collected only from the long-eared sunfish. The bars, anchors, vagina and vaginal tube of this species are distinctive in themselves. One hundred twenty-five hosts from the Embarrass River in April, May, June, July, and August, 1936, were infested one hundred per cent with this parasite.

Genus *Urocleidus* Mueller, 1934

Diagnosis.—Tetraonchinae with intestine bifurcate but confluent posteriorly. Vagina and seminal receptacle lacking. Copulatory complex weakly developed and consisting of an accessory piece and cirrus. Accessory piece not articulated to cirrus base. Haptor subdiscoidal, pentagonal, or hexagonal in shape. Each of the fourteen hooks present may be solid or hollow, with a sickle-shaped structure and opposable piece distally; or consist of a base, shaft, sickle-shaped structure, and opposable piece. Parasitic on the gills of fresh-water fishes. Type species *Urocleidus aculeatus* (Van Cleave and Mueller, 1932).

Urocleidus umbraensis sp. nov.

Figs. 159-165

Host and Locality: Top Minnow (*Fundulus notatus*), Embarrass River, Urbana, Ill.

Location: Gills.

Specimens: U.S.N.M. Helm. Coll. No. 9146.

General anatomy.—Relatively small parasites devoid of surface scales and internal spicules. Average length 0.546 mm. (0.508-0.623 mm.), greatest body width average 0.123 mm. (0.090-0.140 mm.). Haptor distinct, subdiscoidal to hexagonal in shape and broadly connected to the short peduncle. Ventral bar variable in shape, length 0.025 mm. (0.023-0.027 mm.), average length of dorsal bar 0.023 mm. (0.021-0.026 mm.). Anchors similar in shape, bases slightly bifurcate, superficial roots longer than deep roots, wings clearly evident. Each anchor shaft with a small cavity proximally, regularly recurved without formation of angle at junction with points. Bases of ventral anchors wider than dorsal anchor bases. Average length of ventral anchors 0.023 mm. (0.021-0.025 mm.), average length of dorsal anchors 0.022 mm. (0.019-0.024 mm.). Each hook

consists of a slender shaft, sickle-shaped termination and opposable piece. Hook lengths 0.010-0.013 mm. The arrangement of the hooks is as described for the North American fresh-water Tetraonchinae possessing fourteen haptor al hooks (see pages 9, 15, and 62). Anterior eye spots smaller and farther apart than members of the posterior pair.

Reproductive system.—Gonads situated anteriorly in posterior body half; vas deferens passes forward as a slightly undulant tube. Copulatory complex weakly developed and situated in a small vestibule. Cirrus a curved chitinous tube, tapered distally, length 0.025 mm. (0.019-0.030 mm.). Accessory piece a chitinous structure of variable shape. Operation of copulatory complex not observed.

Egg pore on ventral surface anterior to base of copulatory complex. Vagina and seminal receptacle lacking. Vitellaria and vitelline ducts exist as described in the general morphology of the North American fresh-water Tetraonchinae. Nature of shell gland not determined.

Digestive and excretory systems.—The digestive and excretory systems are as given in the general morphology of the North American fresh-water Tetraonchinae. Average diameter of pharynx 0.032 mm. (0.029-0.038 mm.).

Systematic position.—This species has been collected only from the gills of *Fundulus notatus* and is the only monogenetic fluke recorded for this host. *Urocleidus umbraensis* multiplies readily on hosts confined in aquaria. Hosts from natural waters present a low infestation with this parasite.

Genus *Dactylogyrus* Diesing, 1850

Synonym: *Gyrodactylus* Monticelli, 1892, in part.

Diagnosis.—Dactylogyridae with intestine bifurcate but usually confluent posteriorly. Vagina present or absent. Copulatory complex well developed. Haptor moderately developed. One pair of anchors present with bases connected by one or two chitinous bars. Fourteen hooks present on haptor. Four eye spots of approximately the same size in head region. Parasitic on the gills of fishes. Type species, *Dactylogyrus auriculatus* (v. Nordmann, 1832) Diesing, 1850.

Dactylogyrus bychowskyi Mizelle, 1937

Figs. 118-122

Host and Localities: Blunt-Nosed Minnow (*Hyborhynchus notatus*), Embarrass River and Drainage Ditch, Urbana, Ill.

Location: Gills.

Specimens: U.S.N.M. Helm. Coll. No. 9143.

General anatomy.—Relatively small gill trematodes of a somewhat

fusiform nature. Average length 0.381 mm. (0.285-0.615 mm.), average width at level of cephalic lobes 0.057 mm. (0.040-0.086 mm.), greatest body width average 0.079 mm. (0.049-0.108 mm.), average width of peduncle at junction with haptor 0.044 mm. (0.030-0.067 mm.). Haptor distinct, knob-like, at times assuming a subpentagonal shape and broader than long; average width 0.072 mm. (0.050-0.095 mm.), average length 0.059 mm. (0.048-0.068 mm.). The single pair of anchors is located dorsally with their superficial bases connected by a solid chitinous bar. Bases of anchors bifurcate, superficial root noticeably longer than deep root. Anchor shafts (solid in fresh preparations, small cavity in permanent mounts) make junction with points to form a distinct internal angle. Wings on anchor shafts clearly visible. Average length of anchors 0.048 mm. (0.038-0.057 mm.), average width of anchor bases 0.020 mm. (0.015-0.028 mm.). A ventral bar or "ventrales Chitinstuck" or "Chitin-klammer" of German workers, has not been observed in this species. Average length of dorsal bar 0.021 mm. (0.017-0.025 mm.). Each of the fourteen hooks present is differentiated into a base, shaft, sickle-shaped termination and opposable piece. Hook bases ovate and very short as compared with length of shafts. Hooks of pairs numbers one and five slightly shorter than rest of hooks. The arrangement of the hooks is as given in the general morphology of the North American fresh-water Tetraonchinae possessing fourteen haptoral hooks (see pages 9, 15, and 62).

<i>Hook pair</i>	<i>Average length in mm.</i>	<i>Range in mm.</i>
1	0.015	0.013-0.017
2	0.017	0.015-0.019
3	0.017	0.015-0.019
4	0.018	0.015-0.021
5	0.014	0.011-0.017
6	0.017	0.013-0.021
7	0.017	0.015-0.019

Eye spots four in number, approximately equal in size and with members of each pair about the same distance apart.

Reproductive system.—Gonads located near middle of body, testis ovate, situated dorsoposterior to and smaller than ovary. Vas deferens passes forward near the median line of the body as a slightly undulant tube. Seminal vesicle lies near the copulatory complex base and consists of an elongate dilatation of the vas deferens. Two prostate glands present near copulatory complex base, one bulbular in shape, the other botuliform, each emptying into cirrus base by a single individual duct. Copulatory complex well developed and situated in a relatively large vestibule. Cirrus an elongate hollow chitinous tube tapering to a point distally and with a digitiform projection arising from the base. Average length of cirrus

0.044 mm. (0.038-0.051.). Accessory piece a solid chitinous blade-like structure with a knob present about half-way its length. Proximal portion of accessory piece articulated with base of cirrus.

Ovary ovate, larger than testis and with spatial relationships as given above. Egg pore located on ventral surface in the region of the copulatory complex. Vagina present on right body margin in posterior portion of anterior body half. Vaginal tube chitinous and connected with a small clear ovate seminal receptacle. Vitellaria and vitelline ducts as given in the general morphology of the North American fresh-water Tetraonchinae.

Digestive and excretory systems.—Digestive and excretory systems as given in the general morphology of the North American fresh-water Tetraonchinae. Average diameter of pharynx 0.038 mm. (0.029-0.048 mm.).

Systematic position.—*Dactylogyrus bychowskyi* possesses a copulatory apparatus similar to that of *Dactylogyrus amphibothrium* Wagener, 1857, but is different from the latter species in the possession of a digitiform process on the cirrus base. The anchors, hooks, and bars of the two species differ in shape and size relationships. *D. amphibothrium* is found on *Acerina cernua* whereas *D. bychowskyi* occurs on *Hyborhynchus notatus*.

Dactylogyrus bifurcatus Mizelle, 1937

Figs. 123-128

Host and Localities: Blunt-Nosed Minnow (*Hyborhynchus notatus*), Embarrass River and Drainage Ditch, Urbana, Ill.

Location: Gills.

Specimens: U.S.N.M. Helm. Coll. No. 9144.

General anatomy.—Relatively small gill trematodes of a somewhat fusiform nature. Average length 0.343 mm. (0.254-0.492 mm.), average width at level of cephalic lobes 0.051 mm. (0.038-0.065 mm.), greatest body width average 0.070 mm. (0.049-0.095 mm.), average width of peduncle at junction with haptor 0.038 mm. (0.019-0.042 mm.). Haptor distinct, subdiscoidal in shape and broader than long, average width 0.062 mm. (0.049-0.087 mm.), average length 0.044 mm. (0.023-0.057 mm.). The single pair of anchors is located dorsally with their superficial bases connected by a solid chitinous bar. Bases of anchors bifurcate, superficial root longer than deep root. Anchor shafts (solid in fresh preparations, small cavity in permanent mounts) regularly recurved without formation of an angle at junction of shafts and anchors. Wings on anchor shafts clearly visible. Average length of anchors 0.033 mm. (0.028-0.034 mm.), average width of anchor bases 0.012 mm. (0.008-0.013 mm.). Ends of ventral bar slightly bent posteriorly with a short median projection on anterior border and about the same length as dorsal

bar. Average length of dorsal bar 0.017 mm. (0.015-0.023 mm.). Each of the fourteen hooks present is differentiated into a base, shaft, sickle-shaped termination and opposable piece. Hook bases elongate and nearly as long as the shafts. Hooks of pair number one slightly shorter than the rest of the hooks. The arrangement of the hooks is as given in the general morphology of the North American fresh-water Tetraonchinae possessing fourteen haptoral hooks (see pages 9, 15, and 62).

<i>Hook pair</i>	<i>Average length in mm.</i>	<i>Range in mm.</i>
1	0.016	0.013-0.019
2	0.018	0.015-0.021
3	0.019	0.015-0.023
4	0.018	0.015-0.021
5	0.017	0.015-0.019
6	0.018	0.013-0.019
7	0.017	0.015-0.019

Eye spots four in number, about the same size and with members of the two pairs about the same distance apart.

Reproductive system.—Gonads situated near middle of body, testis globular, located posterior to and much larger than ovary. Vas deferens passes forward near median line of body as a slightly undulant tube. Seminal vesicle near copulatory complex and consists of an elongate dilatation of vas deferens. The single prostate gland which lies near the copulatory complex base is bulbular in shape. Copulatory complex well developed and situated in a small vestibule. Cirrus a short curved chitinous tube tapering to a point distally. Average length of cirrus 0.029 mm. (0.027-0.030 mm.). Accessory piece a solid chitinous structure bifurcate distally and with the proximal portion articulated to cirrus base.

Ovary ovate, smaller than testis and with spatial relationships as given above. Egg pore located on ventral surface in region of copulatory complex. The vagina and seminal receptacle have not been observed in this species. Vitellaria and vitelline ducts as given in the general morphology of the North American fresh-water Tetraonchinae.

Digestive and excretory systems.—Digestive and excretory systems as given in the general morphology of the North American fresh-water Tetraonchinae. Average diameter of pharynx 0.022 mm. (0.019-0.027 mm.).

Systematic position.—The morphology of *Dactylogyrus bifurcatus* conforms with the general generic morphology, but differs from other members of the genus by the possession of a short distally bifurcate accessory piece.

Dactylogyrus simplex Mizelle, 1937

Figs. 129-134

Host and Localities: Blunt-Nosed Minnow (*Hyborhynchus notatus*), Embarrass River and Drainage Ditch, Urbana, Ill.

Location: Gills.

Specimens: U.S.N.M. Helm. Coll. No. 9145.

General anatomy.—Relatively small gill trematodes of a general fusiform shape. Average length 0.324 mm. (0.189-0.443 mm.), average width at level of the cephalic lobes 0.045 mm. (0.038-0.057 mm.), greatest body width average 0.062 mm. (0.044-0.076 mm.), average width of peduncle at junction with haptor 0.036 mm. (0.023-0.048 mm.). Haptor distinct, irregularly discoidal in shape, and broader than long, average width about 0.056 mm. (0.042-0.074 mm.), average length about 0.038 mm. (0.029-0.048 mm.). The single pair of anchors is located dorsally with their superficial bases connected by a solid chitinous bar. Bases of anchors bifurcate, superficial root longer than deep root. Anchor shafts solid and regularly recurved without formation of an angle at junction of shafts and points. Wings on anchor shafts clearly discernible. Average length of anchors 0.028 mm. (0.027-0.034 mm.), average width of anchor bases 0.012 mm. (0.008-0.017 mm.). Ends of ventral bar bent posteriorly with a short median projection on the anterior border and about same length as dorsal bar. Average length of dorsal bar 0.019 mm. (0.017-0.021 mm.). Each of the fourteen hooks present is differentiated into a base, shaft, sickle-shaped termination, and opposable piece. Hook bases elongate and nearly as long as the shafts. Hooks of pair number one slightly shorter than rest of hooks. The arrangement of the hooks is as given in the general morphology of the North American fresh-water Tetraonchinae possessing fourteen haptoral hooks (see pages 9, 15, and 62).

Hook pair	Average length in mm.	Range in mm.
1	0.015	0.011-0.017
2	0.017	0.015-0.019
3	0.018	0.015-0.023
4	0.017	0.015-0.023
5	0.016	0.011-0.021
6	0.016	0.013-0.017
7	0.017	0.014-0.023

Eye spots four in number, approximately equal in size and with members of each pair about the same distance apart.

Reproductive system.—Gonads situated in first portion of posterior body half. Testis globular, located posterior to and much larger than ovary. Vas deferens passes forward near median line of body as a slightly undulant tube. Seminal vesicle lies near copulatory complex and

consists of a dilatation of vas deferens. Two prostate glands present near copulatory complex base, one bulbular in shape, the other elongate, each emptying into cirrus base by a single individual duct. Copulatory complex well developed and situated in a large vestibule. Cirrus a hollow, sickle-shaped, chitinous tube, tapering to a point distally. Average length of cirrus 0.024 mm. (0.019-0.029 mm.). Accessory piece a solid chitinous structure with a knob present near the midlength. The proximal portion of the accessory piece is articulated with the base of the cirrus.

Ovary ovate, smaller than testis and with spatial relationships as given above. Egg pore located on ventral surface in region of copulatory complex. The vagina and seminal receptacle are not clearly discernible in this form. Vitellaria and vitelline ducts as given in the general morphology of the North American fresh-water Tetraonchinae.

Digestive and excretory systems.—Digestive and excretory systems as given in the general morphology of the North American fresh-water Tetraonchinae. Average diameter of pharynx 0.022 mm. (0.019-0.025 mm.).

Systematic position.—*Dactylogyrus simplex* is closely related morphologically to *Dactylogyrus anchoratus* (Dujardin, 1845); *Dactylogyrus intermedius* Wegener, 1909; and *Dactylogyrus macracanthus* Wegener, 1909. *Dactylogyrus simplex* differs from these three related species in the shape and size relationships of the copulatory complex, anchors, bars, and hooks. *D. anchoratus* occurs on *Carassius carassius*, *Carassius auratus*, and *Cyprinus carpio*; *D. intermedius* on *Carassius carassius*; *D. macracanthus* on *Tinca tinca*; and *D. simplex* on *Hyborhynchus notatus*.

Dactylogyrus atromaculatus sp. nov.

Figs. 154-158

Host and Locality: Creek Chub (*Semotilus atromaculatus*), Embarrass River, Urbana, Ill.

Location: Gills.

Specimens: U.S.N.M. Helm. Coll. No. 9148.

General anatomy.—Relatively small gill trematodes of a somewhat fusiform nature. Average length 0.526 mm. (0.385-0.656 mm.), greatest body width average 0.089 mm. (0.080-0.103 mm.). Haptor hexagonal or subdiscoidal, and well set off from the body. The single pair of anchors is located dorsally with their superficial bases connected by a solid chitinous bar. Bases of anchors bifurcate, superficial root noticeably longer than deep root. Anchor shafts solid and regularly recurved without formation of internal angle at junction with points. Wings on anchor shafts clearly visible. Average length of anchors 0.033 mm. (0.029-0.040 mm.). A ventral bar, "ventrales Chitinstück" or "Chitinklammer" of German workers, has not been observed for this species. Length of

dorsal bar about length of anchors. Each of the fourteen hooks present is differentiated into a base, shaft, sickle-shaped termination and opposable piece. Hook bases elongate-ovate and shorter than the shafts. Hooks similar in shape and size, lengths 0.017-0.025 mm. The arrangement of the hooks is as given in the general morphology of the North American fresh-water Tetraonchinae possessing fourteen haptor al hooks (see pages 9, 15, and 62). Eye spots four in number, approximately equal in size and with members of each pair about the same distance apart.

Reproductive system.—Gonads located near middle of body, testis ovate; vas deferens passes forward near the median line of the body as a slightly undulant tube. Copulatory complex well developed and situated in a relatively large vestibule. Cirrus an elongate hollow chitinous tube tapered distally. Average length of cirrus 0.037 mm. (0.025-0.042 mm.). Accessory piece a solid chitinous blade-like structure with an enlargement near the midlength. Proximal portion of accessory piece articulated with base of cirrus.

Egg pore located on ventral surface in the region of the copulatory complex. Vagina not clearly distinguishable. Vitellaria and vitelline ducts as given in the general morphology of the North American fresh-water Tetraonchinae.

Digestive and excretory systems.—Digestive and excretory systems as given in the general morphology of the North American fresh-water Tetraonchinae. Average diameter of pharynx 0.031 mm. (0.029-0.038 mm.).

Systematic position.—This species differs from other described species of *Dactylogyrus* by the nature of the copulatory complex. The anchors are similar to those of *Dactylogyrus simplex* Mizelle, 1937. A vestigial bar is lacking in *Dactylogyrus atromaculatus* n. sp., whereas one is present in *D. simplex*. *D. atromaculatus* has been collected only from the gills of the creek chub. It occurs in mixed infestations with an undescribed species of *Dactylogyrus*.

ECONOMIC IMPORTANCE

Trematodes are found abundantly in and on both marine and fresh-water fishes. That they cause serious damage to the host is demonstrated by the work of several authors. The results of Cross (1935) on four-year-old yellow perch (*Perca flavescens*) show that fish with light infestations averaged eighteen per cent longer and one hundred twenty per cent heavier than fish with heavy infestations. This work included observations on myxosporidian, cestode, nematode, and copepod parasites,

in addition to the ectoparasitic and endoparasitic trematodes.¹ Bangham (1927) found that larval cestodes (*Proteocephalus ambloplites*) sterilized one hundred fifty small-mouth bass breeders in an Ohio hatchery. Out of three hundred ninety-one fish (*Platygobio gracilis*) Hubbs (1927) found sixty-eight individuals with abnormalities which he attributed to infestation with parasites, chiefly *Proteocephalus* and several species of trematode metacercariae.² The abnormal fish showed an increase in the number of scales, a retention of larval characters, and an average growth retardation of 4.5 mm. in length. In the production of abnormalities, Hubbs considered *Proteocephalus* more important than trematodes, but in a few cases he attributed relative damage to the latter since some abnormally developed individuals harbored heavy infestations of trematodes and only a few specimens of *Proteocephalus*. Van Haitsma (1931) noted death of four out of a lot of nine ducks, which he was inclined to attribute to infestation with *Cotylurus flabelliformis* (Faust). The same author (1931a) observed two experimentally infested suckers whose death he was sure was due to penetration with cercariae of *Diplostomulum flexicaudum* (Cort and Brooks). Van Haitsma (1931a) quoted Blochman as having had the same experience with several fish placed in a tank with eight specimens of *Lymnaea stagnalis* shedding furcocercous cercariae (*Cercaria fissicauda*). Szidat (1927) cited *Diplostomum spathaceum* (Rud.) as being responsible for the death of thousands of *Acerina cernua* and *Leuciscus rutilus*. McCoy (1928) reported death of seven sunfish (*Eupomotis gibbosus*) by penetration of large numbers of *Cercaria hamata* Miller. Ferguson (unpublished data) in 1936 noted the death of several blunt-nosed minnows (*Hyborhynchus notatus*) experimentally infested with variable numbers of an unidentified furcocercous cercaria from *Physa integra*.

Bangham (1928) is of the opinion that "The internal flukes are probably the least harmful of the bass parasites, but those which are external often do considerable damage to the gills, skin, and fins of the host—especially where they are found in ponds where many bass are confined." Hofer (1904) and Plehn (1924) considered *Gyrodactylus* as destructive to the skin and gills of various species of European fishes. Roth (1922) mentioned this organism as the etiological agent of a contagious disorder of carp, goldfishes, and other fish in aquaria and natural waters. Atkins (1901) recorded *Gyrodactylus elegans* von Nordmann in hatchery ponds and also in the wild waters of Maine. Cooper in 1915 reported *Gyrodactylus medius* Kathariner, on the small-mouth black bass of Canada. Van Cleave (1921) doubted the identity of Cooper's species and

¹Only one specific parasite was mentioned, namely *Triaenophorus nodulosus* (cysts).

²The genus *Proteocephalus* was the only identification made. Hubbs dealt only with endoparasites.

believed it different from any described form. In the same publication Van Cleave described *Gyrodactylus fairporti* in an epidemic from the common bullhead (*Ameiurus melas*) and the European carp (*Cyprinus carpio*) at Fairport, Iowa. Pratt (1929) recorded ectoparasitic helminth infestations on the gills of rainbow trout in the New York Hatchery at Cold Spring Harbor, and mentioned that the parasites were numerous enough in many cases to cause marked damage to the affected hosts. He did not determine the species, but his figure indicated it to be a species of *Gyrodactylus*. Ward (1918) noted the occurrence of *Gyrodactylus* in several localities attacking lake trout and small-mouth bass in the Eastern United States and Canada. Moore (1922) reported it as the causative agent of disease in fish hatcheries in New York, affecting trout primarily, and stated that its range was probably widespread. In 1924 Embury reported *Gyrodactylus* as responsible for considerable loss of trout in New Jersey where measures were undertaken to control its ravages. Hess (1928) noted serious losses in hatcheries among "fry" three to six weeks old by an unidentified species of *Dactylogyrus*. MacCallum (1915) found that members of the family Microcotylidae caused the death of ninety per cent of the angel and butterfly fishes in the tanks of the New York Aquarium. Guberlet, Hansen, and Kavanagh (1927) reported a daily mortality of one to two per cent for rainbow trout fingerlings (*Salmo irideus shasta*) infested with *Gyrodactylus elegans*, in a hatchery near Seattle, Washington, from November 15 to December 20, 1925. Two individuals (observed by the present author) out of a lot of sixteen black crappies (*Pomoxis sparoides*) transported by automobile from Lake Senachwine near Henry, Illinois, showed signs of suffocation and loss of balance on arrival at the laboratory at Urbana, Illinois. These two fish died approximately six hours later in one of the Illinois State Natural History Survey aquaria. On examination they were found heavily infested with *Cleidodiscus capax* Mizelle. The rest of the fish presented no particular symptoms of disease, and when examined at a later date were found to harbor only light infestations of the same species of parasite. It has been observed that yellow bass (*Morone interrupta*), which often harbor several hundreds of *Onchocleidus interruptus* Mizelle, on their gills, die soon after removal from the net when placed in containers filled with aerated water of the same temperature as that from which they were taken. Death of these hosts was prevented by cooling the water in containers before placing the fish therein. During the spring of 1937 an epidemic among blunt-nosed minnows (*Hyborhynchus notatus*) by *Dactylogyrus bychowskyi* Mizelle, was observed. Over three hundred hosts in an aquarium at the University of Illinois died during the epidemic. Steel colored minnows (*Notropis whipplii*) in the same tank were not affected.

The flukes were found to infest the gills of the hosts exclusively. As many as two hundred parasites were recovered from one fish in this epidemic, whereas twenty-five fish examined a few hours after removal from neighboring streams, namely the Drainage Ditch and Embarrass River, harbored an average of five parasites each. It has not as yet been determined whether these phenomena are due wholly to infestation with the specific gill trematodes mentioned. Van Cleave (1921) and Mueller and Van Cleave (1932) are in accord with Bangham (1928) in stating that infestations with ectoparasites are more apt to become serious in aquaria and artificial enclosures rather than in natural waters. The same idea was expressed by MacCallum (1915), but after his publication had gone to press he had occasion to examine several fish from the open sea, two of which were snappers (*Priacanthus cruentatus*), whose death he was certain was due to infestation with *Diplectana*. The present writer has not recorded a single epidemic of tetraonchid ectoparasites among infested sunfishes kept in aquaria for maximum intervals of four weeks. Records of epidemics or serious outbreaks of oviparous *Gyrodactyloidea* are not as numerous as for viviparous forms. Members of the genus *Gyrodactylus*, have been observed to harbor as many as two generations within a single parent.

The nature of damage by ectoparasitic trematodes to fish hosts is varied. MacCallum (1915) attributed the damage of *Microcotyle* to be of a double nature, namely the production of an anemia and suffocation. This author says that species of this genus (*Microcotyle*) fasten themselves to the gills of fishes and that such attachment causes irritation which induces an outflow of mucus covering the gills, thus preventing access of water to the respiratory surfaces. Due to the feeding habits of these parasites, a depletion of the host's blood supply occurs which renders it exsanguine, producing death. MacCallum (1927) recorded that in 1926 Miss Ida Mellen noted the destruction of the cornea of the Pacific puffer (*Spheroides annulatus*), the spade fish (*Chaetodipterus faber*), and several species of angel fishes of the genera *Angelichthys* and *Pomacanthus* by *Epibdella melleni* MacCallum. Tubangui (1931), in regard to *Ancyrocephalus manilensis* Tubangui, stated that the infested organs were much congested and showed numerous punctiform hemorrhages, produced no doubt by the hooks of the parasite. Pratt (1929) mentioned a shriveling of the gills which rendered them functionless in heavy infestations of *Gyrodactylus* on rainbow trout. Van Cleave (1921) considered direct damage to the general body surfaces of fishes by *Gyrodactylus fairporti* Van Cleave, only one mode of parasitic attack and that additional damage was possibly done by bacteria, protozoa, and fungi, whose invasion of the host was made possible by removal of skin and scales by the armature of ectoparasitic helminths.

The present author in examining over one thousand individuals belonging to species of Tetraonchinae and Dactylogyrynae described herein, found infestations restricted to branchial tissues. This site of parasitic attack is in accord with the findings of MacCallum (1915) for the Octocotylidae, Microcotylidae, and *Diplectana*. The principal damage to fish hosts by the observed members of Tetraonchinae is accomplished presumably by an irritative or toxic action resulting from the insertion of the haptor. Each point of haptoral attachment on the branchial filaments of the black and white crappies (*P. sparoides* and *P. annularis*) by *Cleidodiscus capax* Mizelle, and of the bluegill sunfish (*Helioperca macrochira*) by *Cleidodiscus robustus* Mueller, generally present an enlarged circumscribed area denoting an apparent condition of hypertrophy or hyperplasia. These areas become thickly covered with mucus which prevents contact of the branchial surface with the water, recalling the condition of suffocation mentioned by MacCallum (1915) for members of the genus *Microcotyle*.

A knowledge of the specific etiological agent together with its complete life history is indispensable to the successful control of a disease. Until recently the incompleteness of such information concerning the North American Gyrodactyloidea Johnston and Tiegs, has been astonishing. MacCallum (1915 and 1927) described a number of species from marine fishes. Van Cleave (1921) described *Gyrodactylus fairporti* from Fairport, Iowa. Hess (1928 and 1930) recorded the presence of undetermined species of *Dactylogyryus* and *Gyrodactylus* on goldfishes and an undetermined species of *Ancyrocephalus* from several species of native fishes in Indiana and central New York. Stafford (1905), Cooper (1915), Ward (1918), Bangham (1926), and Guberlet, Hansen, and Kavanagh (1927) have given records of one or more instances of the occurrence of Gyrodactyloidea on fresh-water fishes, but have left doubts as to the identity of the forms with which they dealt, and in several instances made identification only to genus. In 1928 Bangham made no attempt to identify species of gill parasites of the large-mouth black bass (*Aplites salmoides*). In 1933 the same author in his publication on the parasites of the spotted bass (*Micropterus pseudaplites*), which also included a summary of parasites of the small and large-mouth basses from Ohio streams, did not record a single ectoparasitic trematode for the spotted or Kentucky bass, and only one unidentified species of *Ancyrocephalus* for the other hosts. Since 1931 taxonomic work on this group has been relatively prolific (see page 13).

In regard to life histories of the Monogenea, only three are completely known. Of the Gyrodactyloidea, the life history of *Gyrodactylus elegans* von Nordmann was studied by Kathariner in 1904. The life history of *Epibdella melleni* MacCallum, belonging to the Capsaloidea, was pub-

lished by Jahn and Kuhn in 1932. Zeller (1872a) published the life history of *Diplozoon paradoxum*, a member of Polyopisthocotylea. Zeller also published (1872) a description of the life history of *Polystomum integerrimum*, but this work has been doubted by many authors including Stunkard (1917). Hess (1928) gave a very superficial account of the life history of an unidentified species of *Dactylogyrus* which he found infesting the gills of the small and large-mouth black basses, common sunfish, goldfish, carp, and "other fishes."

In discussing possibilities of controlling endoparasites, different authors have suggested destruction of a unit in the chain of hosts utilized by a particular species, as a means of extermination of the etiological agent. Chandler (1920) suggested the killing of the snail host (which harbors intermediate stages of trematode parasites) in order to stamp out certain trematode diseases. Linton (1911) advocated the shooting of water birds as a measure for ridding fish of yellow grub or metacercariae of *Clinostomum*. Baker (1922) pointed out the danger of such practices by showing the relationships of Mollusca in food chains of aquatic organisms. In addition Baker called attention to the fact that agents such as copper sulphate used to kill snails were highly toxic to algae and other microscopic life on which higher animals depend for food.

Methods for extermination of monogenetic trematodes must of necessity differ radically from those used for digenetic forms because of a difference in life histories. In the light of our present knowledge, an intermediate host is not utilized by monogenetic flukes. Infection is accomplished by contact (MacCallum, 1927), (Guberlet, Hansen, and Kavanagh, 1927) and when fish are subjected to crowded conditions, ectoparasitic trematodes often increase in numbers that effect a high mortality of the hosts as pointed out by MacCallum (1915), Van Cleave (1921), Guberlet, Hansen, and Kavanagh (1927), and others.

Various methods have been proposed for destruction of these trematodes. Hubner (1895) recommended an exposure of infested fish to a one-fourth of one per cent solution of salicylic acid for thirty minutes. Hofer (1904) also recommended the treatment of Hubner and in addition advocated a bath of one part of potassium permanganate to one hundred thousand parts of water. Plehn (1924) proposed an exposure of diseased fish for ten minutes to a two per cent solution of hydrogen peroxide and subjection to a one to eight thousand acetic acid bath from one to one and one-half hours as being specific for ectoparasites closely related to *Discocotyle salmonis* Schaffer. Davis (1929) found the acetic acid treatment ineffective. Laird and Embury (1931) also found the acetic acid bath of no benefit and determined treatment with a bath of copper sulphate and of saturated sodium chloride solution, as used by European fish culturists for one to one and one-half minutes (Davis

1929), to be worthless. Through an indirect communication, the present author learned that Jahn successfully treated fish for *Epibdella melleni* by doubling the concentration of salt in sea water. Laird (1927) reported successful destruction of gill parasites by spraying the branchial tissue with a twenty per cent solution of Zonite. Laird and Embury (1931) recommended a two minute immersion of fish in a solution of Zonite made of one ounce of the chemical to ten to twelve quarts of water. Guberlet, Hansen, and Kavanagh (1927) found gyrodactyliasis, or fin disease of fish, very difficult to control. After a number of experiments with various chemicals they concluded that exposure to a four and one-half to five per cent solution of common salt for one and one-half to two and one-half minutes to be the safest and most effective treatment for the disease. Hess (1930) found that immersion of the host for two hours in a solution of potassium permanganate (one pound to thirty-two thousand gallons of water) was absolutely specific for undetermined species of *Gyrodactylus* and *Dactylogyrus* on goldfishes. He also recommended spraying the surface of ponds with one pound of the dissolved chemical to twenty-five thousand to forty thousand gallons of water, depending on the amount of organic matter present, capable of reducing potassium permanganate. Hess observed that old fish withstood stronger solutions of this chemical better than did the younger individuals. Because of reduction of potassium permanganate by organic matter in hatchery ponds, this method becomes impractical due to the inability to correctly estimate the amount of organic material in the water. Water capacity of hatchery ponds must also be known for intelligent use of the anthelmintic.

Fish culturists and conservation agencies responsible for rearing and distributing fishes have given practically no attention to the dangers of transporting gill parasites into new regions. Except for a few of the large species, the gyrodactylids are so small as to escape field inspections. Furthermore, detailed information as to the species involved and the specific action of each on the host has been generally lacking. Doubtless the inconsistencies encountered by several authors, with various anthelmintics recommended by other workers, were in part due to the fact that they dealt with ectoparasites other than those for which particular chemicals were found specific. Control measures aimed at a generalized treatment for ectoparasitic trematodes would probably be as meaningless as a generalized therapy for the multitude of human diseases. It is recommended that fishes infested with monogenetic trematodes be subjected to therapy one hundred per cent effective for removal of such parasites, before placing them in new environments as aquaria, fish hatcheries, or natural waters. New hosts for etiological agents of disease generally suffer high mortality until a physiological balance with the organism is established.

DISCUSSION

In a recent publication Mueller (1937) mentioned two systems of numbering the hooks on haptors of fresh-water species of North American Tetraonchinae. Contentions regarding the order of these structures are not of a serious nature, and only for the sake of future workers in this field are the following comparisons and deductions set forth. It must be remembered that any arbitrary system of numbering that deals with haptoral hooks in this group of parasites cannot be regarded as having unquestionable value. A natural system of numbering these hooks must be attained through embryological studies. In the absence of such studies, all systems of numbering must be regarded as highly artificial, derived solely as a matter of convenience, and discarded when basic information is produced. Information concerning the embryology of North American Tetraonchinae is as yet wanting.

Haptoral hooks, in North American fresh-water species of Tetraonchinae (Tetraonchus and Murraytrema not studied) and Dactylogyriinae, are distributed on both dorsal and ventral sides of the haptor, five pairs being on the ventral and two pairs on the dorsal side.¹ In 1936 Mueller numbered the hooks consecutively around the margin of the haptor, beginning with the anterior central (ventral) pair of hooks as number one. Since the two dorsal pairs of hooks are variable in their positional relationships (in different species) with the five pairs of ventral hooks, the earlier proposed system of numbering (Mueller 1936) becomes very confusing. Discrepancies naturally occur in the older system of numbering because of this fluctuation in the linear positions of the two pairs of hooks mentioned. For instance, the most anterior dorsal hook is labelled number six by Mueller for *Onchocleidus mimus* (1936, p. 59, pl. 13, fig. 13), two for *O. similis* (*ibid.*, fig. 10), four for *O. ferox* (*ibid.*, fig. 12) and number five for *P. acer* and *H. dispar* (*ibid.*, figs. 9 and 11), whereas in the new system of numbering (Mizelle, 1936) each anterior dorsal hook consistently becomes number seven for each species. Since the hooks involved (all except number one) are generally identical in structure in a given species, with varying size relationships in different species together with variable spatial relationships with each other, the stable character of ventral and dorsal distribution must be resorted to if any degree of regularity is to be attained. In the later proposed system of numbering (Mizelle, 1936) Mueller's starting point is utilized for hooks of the first pair, but instead of zigzagging in some cases from one surface of the haptor to the other and in other cases going consecutively from

¹In 1936 the present author described a variation of this arrangement for one species, viz., *Actinocleidus articularis* (Mizelle, 1936). All fourteen hooks were thought to occur on the same side of the haptor. In subsequent work, the hook arrangement of all species in this genus has been found to agree with that existing in the other North American Tetraonchinae (fresh-water) genera possessing fourteen haptoral hooks.

ventral to dorsal side with the exclusion of the hook pair in the region of the ventral anchors, the sequence is posteriorly around the ventral side of the haptor and then dorsally in an anterior direction (figs. 173-174). Hooks numbers six and seven always relate to those on the dorsal side of the haptor, number six being invariably the more posterior. The single pair of hooks whose position is in the region of the ventral anchors obviously becomes number five in the new system instead of seven in that of Mueller's.

Mueller (1937) cited *O. mimus* and *Cleidodiscus robustus* as possessing the primitive hook arrangement, whereas in 1936 he referred to *Actinocleidus oculatus* as possessing it. The present writer has found the same basic hook arrangement present in all species examined. The species of *Dactylogyrus* described in this paper possess the same hook arrangement as the Tetraonchinae, and although the ventral pair of anchors has disappeared in this genus, a ventral chitinous structure is present in *D. simplex*, *D. bifurcatus*, and many other previously described species. This structure could very easily be interpreted to represent a remnant of the ventral bar that once connected the two members of the ventral pair of anchors. The genus *Haploleidus* Mueller, 1937, which is characterized by a marked difference in the size of the two pairs of anchors, strongly suggests an intermediate stage in the transition from a condition of four anchors to a condition of two anchors or one pair. The genus *Gyrodactylus* is assumed to be more specialized than either of the foregoing since only one pair of anchors is present without a vestige of the ventral bar; oviparity is replaced by viviparity; eye spots have disappeared in adults; and all the hooks (eight pairs) occur on the same side of the haptor.

The present writer is in general accord with Price (1937a) with reference to the possible invalidity of some of Mueller's recently created genera, viz., *Cleidodiscus*, *Urocleidus*, *Onchocleidus*, *Leptocleidus*, *Tetraclaidus*, *Aristocleidus*, *Haploleidus*, *Pterocleidus*, and *Actinocleidus*. Species of *Urocleidus* are not unlike those of *Onchocleidus* except for the absence of a vagina, a condition which sporadically occurs in several genera of Tetraonchinae. *Leptocleidus* possesses characters common to the genus *Cleidodiscus* with which it is probably synonymous. *Tetraclaidus* is distinguished from *Onchocleidus* (Mueller, 1936) by the presence of an accessory piece in the copulatory complex. This structure has been described for practically all species of *Onchocleidus*. *Aristocleidus* is also like *Onchocleidus* except for a difference of size and shape relationships of the dorsal and ventral anchors, a condition which occurs in other genera of this subfamily. *Haploleidus* was split off the genus *Onchocleidus* to include forms which possess dorsal anchors that are much larger than the ventral anchors. Recent research (Seamster, 1938)

has shown this condition to occur as a variation in *Cleidodiscus pricei* Mueller, 1936. *Pterocleidus* was also split off the genus *Onchocleidus* and made to include forms which possess a spur on each anchor shaft. This condition is thought to be of no more importance than occurrence of spines on the bars of *Onchocleidus mucronatus* Mizelle, *O. cyanellus* Mizelle, *Cleidodiscus vancleavei* Mizelle, and *C. robustus* Mueller. The genus *Actinocleidus* was taken from *Cleidodiscus* to embrace forms which have fused bars and both pairs of anchors on the same side of the haptor. This genus is held as valid. A revision of the North American fresh-water genera of Tetraonchinae is contemplated in the near future.

SUMMARY

A method has been perfected for removal of ninety-two per cent of the monogenetic flukes present on the gills of fresh-water fishes.

Successful attachment of small gyrodactyloid parasites to glass slides, to prevent loss of such material during technical processes requisite for production of permanent mounts, has been accomplished.

Twenty-one species of monogenetic trematodes of the subfamilies Tetraonchinae and Dactylogyrynae have been described from the gills of Illinois fishes. A few host records are reported from Oklahoma.

A review of the detrimental effects of monogenetic trematodes to fish hosts, together with a review of control methods for these parasites, is given.

A thorough subjection of fish hosts, infested with monogenetic trematodes, to procedures requisite for one hundred per cent removal of all stages of such parasites, is recommended before transplanting them in new environments, as aquaria, fish hatcheries, or natural waters.

Chitinous parts as anchors, bars, hooks, and copulatory structures are relatively constant and serve for definite identification of species of fresh-water Gyrodactyloidea especially when host-parasite relationships are known.

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PLATES

All figures were drawn with the aid of a camera lucida (except 173 and 174 which are diagrammatic). The scale used is indicated on each plate.

PLATE I

- FIG. 1.—*Cleidodiscus robustus* Mueller, 1934.
 FIG. 2.—*Onchocleidus interruptus* Mizelle, 1936.
 FIG. 3.—*Onchocleidus principalis* Mizelle, 1936.
 FIG. 4.—*Cleidodiscus longus* Mizelle, 1936.
 FIG. 5.—*Cleidodiscus vancleavei* Mizelle, 1936.
 FIG. 6.—*Cleidodiscus bedardi* Mizelle, 1936.

Abbreviations

<i>CC</i>	Copulatory complex	<i>PH</i>	Pharynx
<i>CL</i>	Cephalic lobe	<i>SG</i>	Shell gland
<i>ES</i>	Eye spots	<i>SR</i>	Seminal receptacle
<i>GC</i>	Cephalic glands	<i>SV</i>	Seminal vesicle
<i>H</i>	Haptor	<i>T</i>	Testis
<i>HO</i>	Head organs	<i>UP</i>	Egg or uterine pore
<i>IC</i>	Intestinal crura	<i>UT</i>	Oviduct or uterus
<i>M</i>	Mouth	<i>V</i>	Vagina
<i>OV</i>	Ovary	<i>VD</i>	Vas deferens
<i>P₁</i>	Prostate containing finely granular hyaline fluid	<i>VDT</i>	Vitelline duct
<i>P₂</i>	Prostate containing coarsely granular yellowish fluid	<i>VIT</i>	Vitellaria

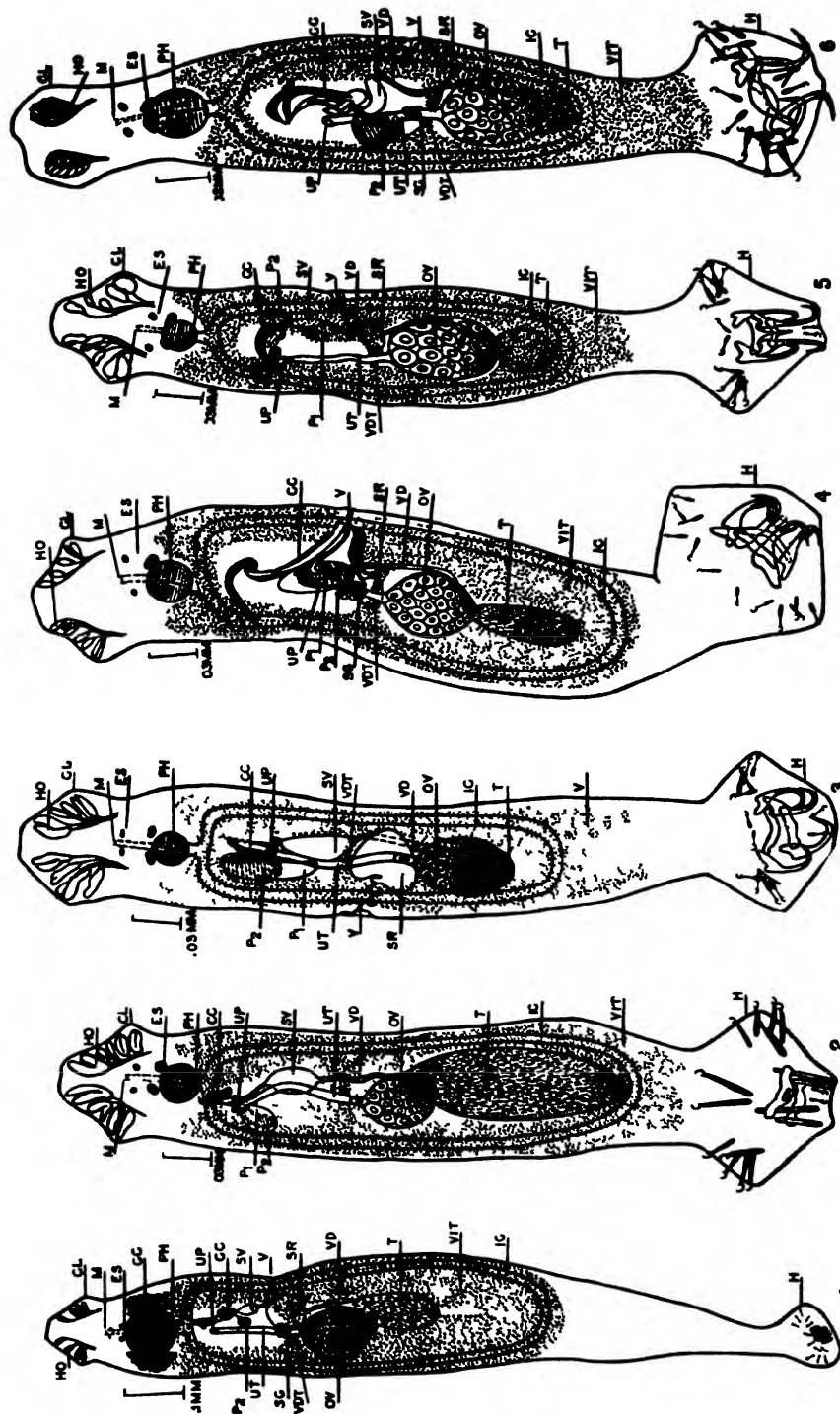


PLATE I

PLATE II

Abbreviations same as for Plate I

- FIG. 7.—*Cleidodiscus capax* Mizelle, 1936.
FIG. 8.—*Onhocleidus distinctus* Mizelle, 1936.
FIG. 9.—*Onhocleidus mucronatus* Mizelle, 1936.
FIG. 10.—*Actinocleidus articularis* (Mizelle, 1936).
FIG. 11.—*Pterocleidus acuminatus* (Mizelle, 1936).
FIG. 12.—*Cleidodiscus uniformis* Mizelle, 1936.

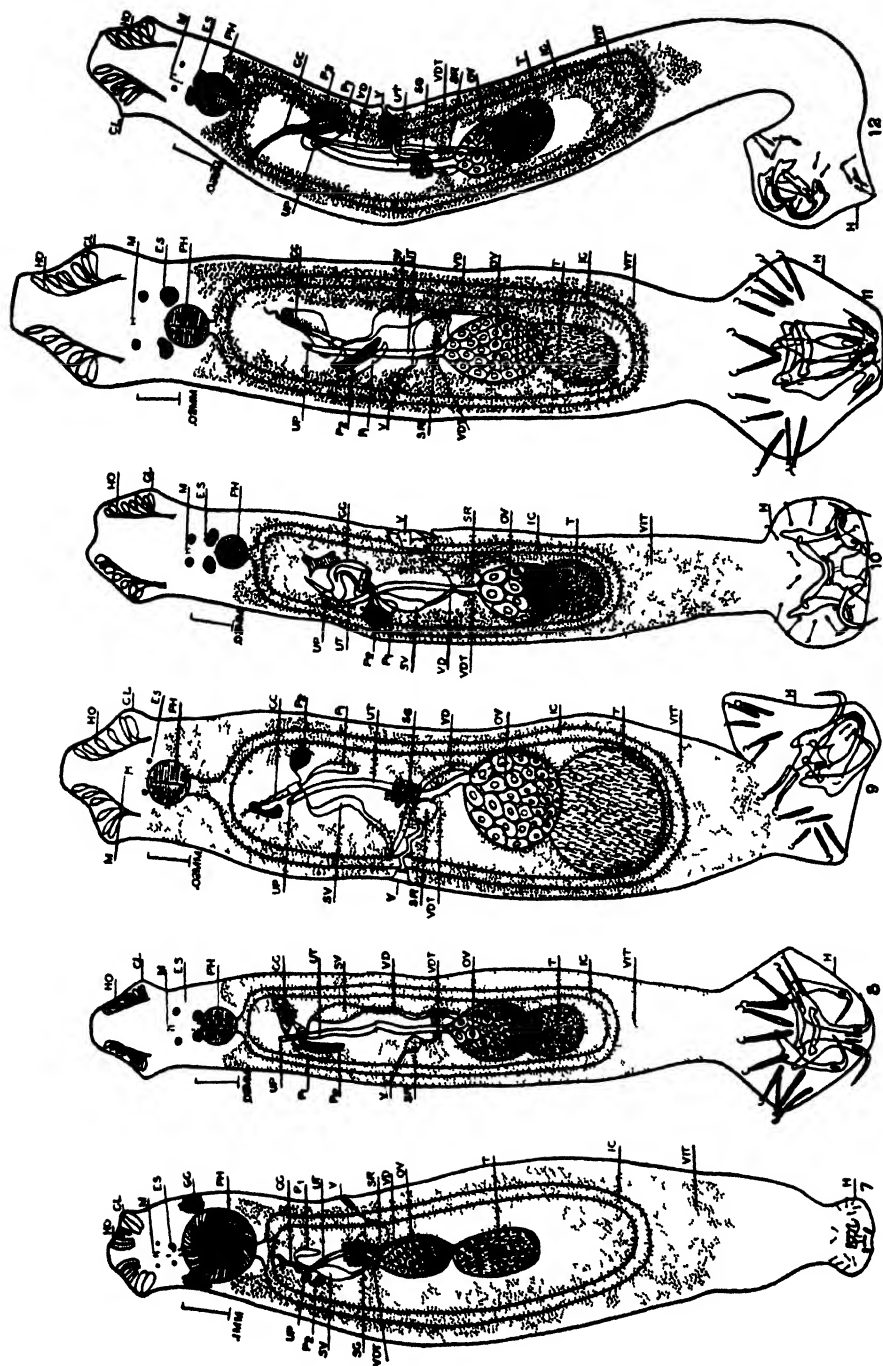


PLATE II

PLATE III

Cleidodiscus robustus Mueller, 1934

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|---------------------------------|--------------------------|
| FIG. 13. Accessory piece. | FIG. 18.—Dorsal anchor. |
| FIG. 14.—Cirrus. | FIG. 19.—Ventral anchor. |
| FIG. 15.—Vagina. | FIG. 20.—Dorsal bar. |
| FIG. 16.—Vaginal tube or canal. | FIG. 21.—Ventral bar. |
| FIG. 17.—Seminal receptacle. | |

Onchocleidus mucronatus Mizelle, 1936

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|---------------------------|---------------------------------|
| FIG. 22.—Cirrus. | FIG. 27.—Ventral bar. |
| FIG. 23.—Accessory piece. | FIG. 28.—Vagina. |
| FIG. 24.—Dorsal anchor. | FIG. 29.—Vaginal tube or canal. |
| FIG. 25.—Ventral anchor. | FIG. 30.—Seminal receptacle. |
| FIG. 26.—Dorsal bar. | |

Cleidodiscus vancleavei Mizelle, 1936

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|---------------------------|---------------------------------|
| FIG. 31.—Accessory piece. | FIG. 36.—Vaginal tube or canal. |
| FIG. 32.—Cirrus. | FIG. 37.—Seminal receptacle. |
| FIG. 33.—Dorsal anchor. | FIG. 38.—Dorsal bar. |
| FIG. 34.—Ventral anchor. | FIG. 39.—Ventral bar. |
| FIG. 35.—Vagina. | |

Actinocleidus articularis (Mizelle, 1936)

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|----------------------------|---------------------------------|
| FIG. 40.—Anterior anchor. | FIG. 45.—Vaginal tube or canal. |
| FIG. 41.—Anterior bar. | FIG. 46.—Seminal receptacle. |
| FIG. 42.—Posterior anchor. | FIG. 47.—Accessory piece. |
| FIG. 43.—Posterior bar. | FIG. 48.—Cirrus. |
| FIG. 44.—Vagina. | |

Cleidodiscus longus Mizelle, 1936

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|---|---------------------------------|
| FIG. 49.—Dorsal bar. | FIG. 53.—Vaginal tube or canal. |
| FIG. 50.—Ventral bar. | FIG. 54.—Seminal receptacle. |
| FIG. 51.—Cirrus and accessory
piece. | FIG. 55.—Dorsal anchor. |
| FIG. 52.—Vagina. | FIG. 56.—Ventral anchor. |

Cleidodiscus bedardi Mizelle, 1936

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|---------------------------|---------------------------------|
| FIG. 57.—Dorsal bar. | FIG. 62.—Ventral anchor. |
| FIG. 58.—Ventral bar. | FIG. 63.—Vagina. |
| FIG. 59.—Cirrus. | FIG. 64.—Pseudovagina. |
| FIG. 60.—Accessory piece. | FIG. 65.—Vaginal tube or canal. |
| FIG. 61.—Dorsal anchor. | FIG. 66.—Seminal receptacle. |

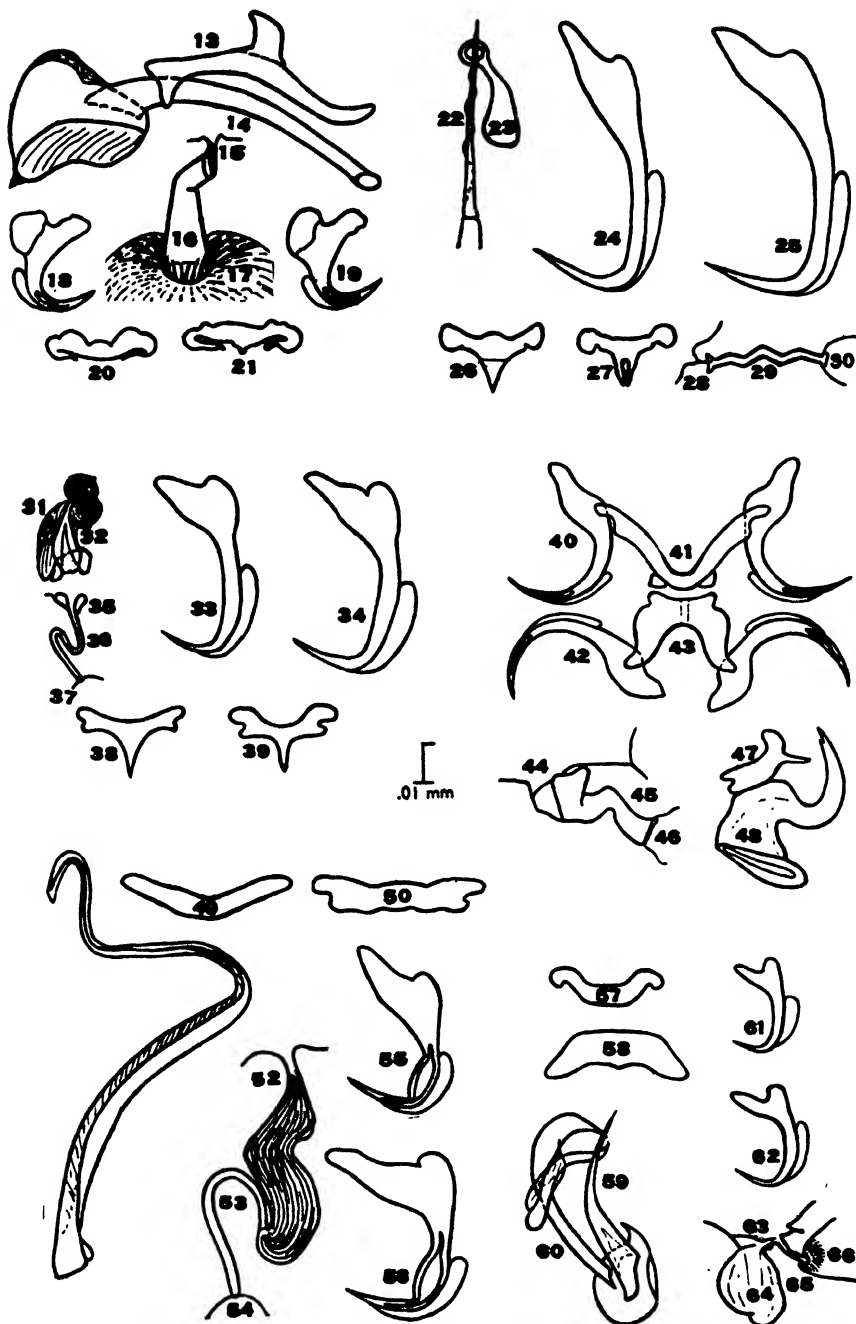


PLATE III

PLATE IV

Cleidodiscus capax Mizelle, 1936

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|---------------------------|---------------------------------|
| FIG. 67.—Accessory piece. | FIG. 72.—Vaginal tube or canal. |
| FIG. 68.—Cirrus. | FIG. 73.—Seminal receptacle. |
| FIG. 69.—Dorsal anchor. | FIG. 74.—Dorsal bar. |
| FIG. 70.—Ventral anchor. | FIG. 75.—Ventral bar. |
| FIG. 71.—Vagina. | |

Onchocleidus principalis Mizelle, 1936

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|---------------------------------|---------------------------|
| FIG. 76.—Dorsal anchor. | FIG. 81.—Accessory piece. |
| FIG. 77.—Ventral anchor. | FIG. 82.—Cirrus. |
| FIG. 78.—Vagina. | FIG. 83.—Dorsal bar. |
| FIG. 79.—Vaginal tube or canal. | FIG. 84.—Ventral bar. |
| FIG. 80.—Seminal receptacle. | |

Cleidodiscus uniformis Mizelle, 1936

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|---------------------------|---------------------------------|
| FIG. 85.—Dorsal bar. | FIG. 90.—Cirrus. |
| FIG. 86.—Ventral bar. | FIG. 91.—Vagina. |
| FIG. 87.—Dorsal anchor. | FIG. 92.—Vaginal tube or canal. |
| FIG. 88.—Ventral anchor. | FIG. 93.—Seminal receptacle. |
| FIG. 89.—Accessory piece. | |

Pterocleidus acuminatus (Mizelle, 1936)

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|---------------------------------|---------------------------|
| FIG. 94.—Dorsal bar. | FIG. 99.—Accessory piece. |
| FIG. 95.—Ventral bar. | FIG. 100.—Cirrus. |
| FIG. 96.—Vagina. | FIG. 101.—Dorsal anchor. |
| FIG. 97.—Vaginal tube or canal. | FIG. 102.—Ventral anchor. |
| FIG. 98.—Seminal receptacle. | |

Onchocleidus interruptus Mizelle, 1936

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|----------------------------|---------------------------|
| FIG. 103.—Dorsal anchor. | FIG. 106.—Ventral anchor. |
| FIG. 104.—Cirrus. | FIG. 107.—Dorsal bar. |
| FIG. 105.—Accessory piece. | FIG. 108.—Ventral bar. |

Onchocleidus distinctus Mizelle, 1936

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|----------------------------|----------------------------------|
| FIG. 109.—Dorsal bar. | FIG. 114.—Vagina. |
| FIG. 110.—Ventral bar. | FIG. 115.—Vaginal tube or canal. |
| FIG. 111.—Dorsal anchor. | FIG. 116.—Seminal receptacle. |
| FIG. 112.—Accessory piece. | FIG. 117.—Ventral anchor. |
| FIG. 113.—Cirrus. | |

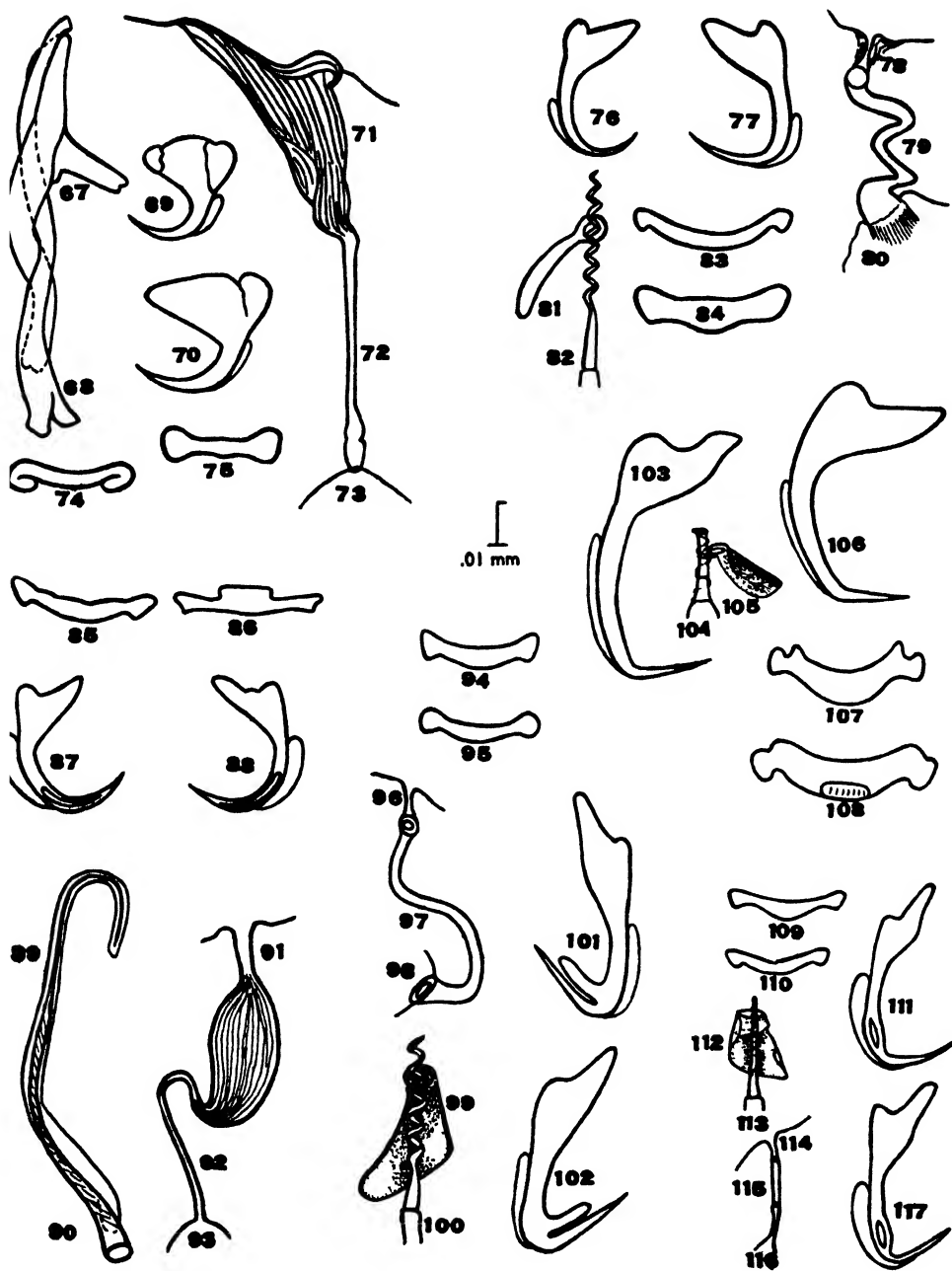


PLATE IV

PLATE V

Dactylogyrus bychowskyi Mizelle, 1937

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|-------------------|----------------------------|
| FIG. 118.—Anchor. | FIG. 121.—Accessory piece. |
| FIG. 119.—Bar. | FIG. 122.—Hooks. |
| FIG. 120.—Cirrus. | |

Dactylogyrus bifurcatus Mizelle, 1937

- | | |
|----------------------------|-------------------|
| FIG. 123.—Dorsal bar. | FIG. 126.—Cirrus. |
| FIG. 124.—Accessory piece. | FIG. 127.—Anchor. |
| FIG. 125.—"Ventral bar." | FIG. 128.—Hooks. |

Dactylogyrus simplex Mizelle, 1937

- | | |
|-----------------------|----------------------------|
| FIG. 129.—Anchor. | FIG. 132.—"Ventral bar." |
| FIG. 130.—Hooks. | FIG. 133.—Accessory piece. |
| FIG. 131.—Dorsal bar. | FIG. 134.—Cirrus. |

Onchocleidus cyanellus n. sp.

- | | |
|-------------------------------|--------------------------|
| FIG. 135.—Ventral anchor. | FIG. 138.—Hook. |
| FIG. 136.—Copulatory complex. | FIG. 139.—Ventral bar. |
| FIG. 137.—Dorsal bar. | FIG. 140.—Dorsal anchor. |

Cleidodiscus diversus n. sp.

- | | |
|----------------------------|------------------------|
| FIG. 141.—Dorsal anchor. | FIG. 145.—Dorsal bar. |
| FIG. 142.—Accessory piece. | FIG. 146.—Ventral bar. |
| FIG. 143.—Cirrus. | FIG. 147.—Hook. |
| FIG. 144.—Ventral anchor. | |

Actinocleidus fergusonii n. sp.

- | | |
|-----------------------------|----------------------------|
| FIG. 148.—Anterior anchor. | FIG. 151.—Posterior bar. |
| FIG. 149.—Anterior bar. | FIG. 152.—Accessory piece. |
| FIG. 150.—Posterior anchor. | FIG. 153.—Cirrus. |

Dactylogyrus atromaculatus n. sp.

- | | |
|----------------------------|-------------------|
| FIG. 154.—Cirrus. | FIG. 157.—Hook. |
| FIG. 155.—Accessory piece. | FIG. 158.—Anchor. |
| FIG. 156.—Bar. | |

Urocleidus umbraensis n. sp.

- | | |
|----------------------------|------------------------|
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| FIG. 160.—Ventral anchor. | FIG. 164.—Ventral bar. |
| FIG. 161.—Accessory piece. | FIG. 165.—Hook. |
| FIG. 162.—Cirrus. | |

Actinocleidus longus n. sp.

- | | |
|-----------------------------|----------------------------|
| FIG. 166.—Anterior anchor. | FIG. 170.—Hook. |
| FIG. 167.—Anterior bar. | FIG. 171.—Accessory piece. |
| FIG. 168.—Posterior anchor. | FIG. 172.—Cirrus. |
| FIG. 169.—Posterior bar. | |

FIGS. 173-174.—Side and ventral views of haptors to show arrangement of hooks.

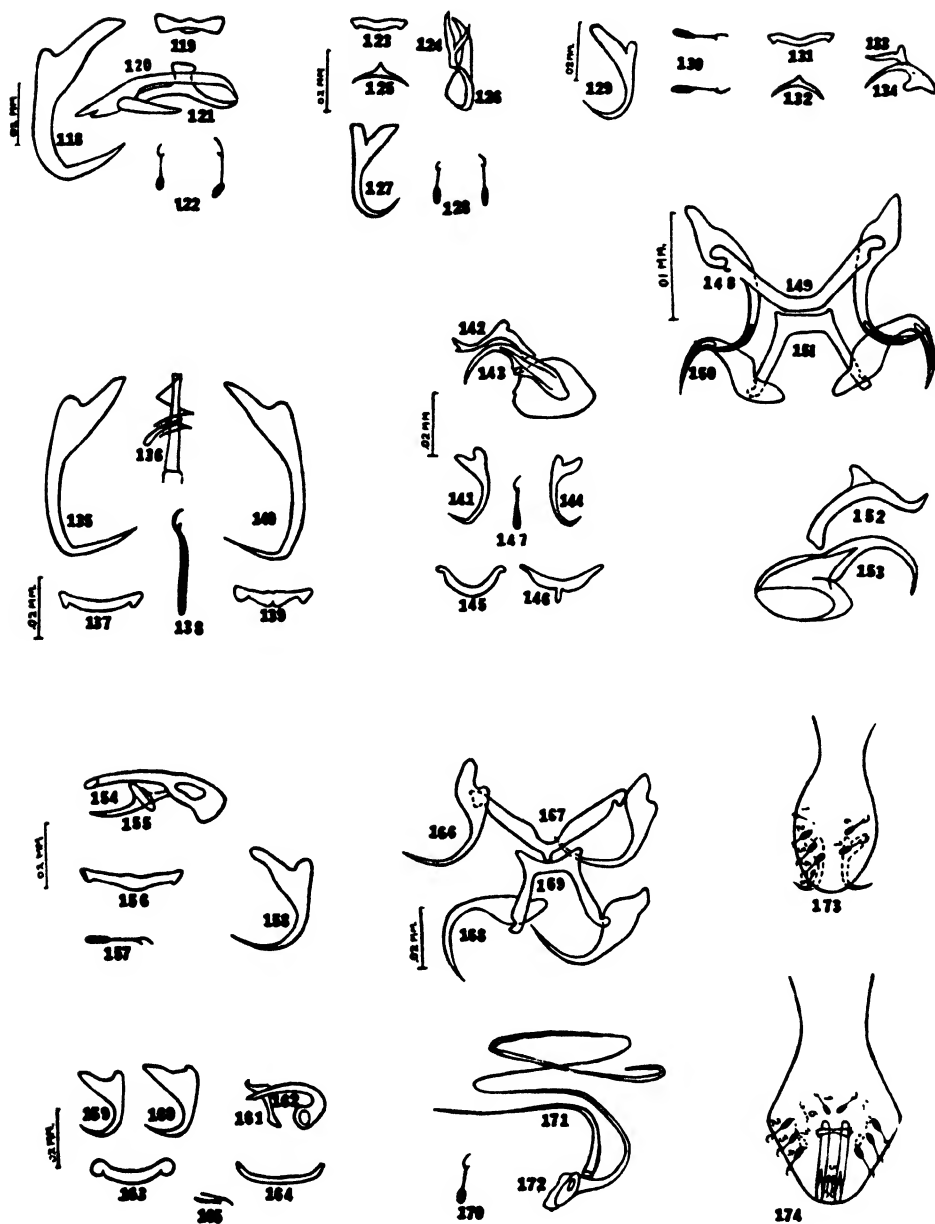


PLATE V

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THE MICROTHYRIACEAE

BY
FRANK LINCOLN STEVENS
AND
SISTER MARY HILAIRE RYAN, O.P.

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PREFACE

For a number of years prior to his death, which occurred on the sixteenth day of August, 1934, Dr. Frank Lincoln Stevens, Professor of Plant Pathology at the University of Illinois, was engaged in an intensive study of the Microthyriaceae, parasitic fungi which infest the leaves of tropical and sub-tropical plants. Because of frequent attacks of angina pectoris, Dr. Stevens feared he might not live to complete his manuscript. It was then that he requested the writer to finish his work in the event of his untimely death. Such a request from this eminent scientist, to whom the writer was greatly indebted, could not be refused, especially since she hoped that God would spare him to complete his task.

Three months after Dr. Stevens' death, the manuscript arrived at Rosary College. A note from Mrs. Stevens said that she had found the memorandum of the above request among her husband's papers. It has been a pleasure and a privilege to carry on the work of our beloved Dr. Stevens.

For Dr. Stevens and for myself, I offer our many friends hearty thanks for the valuable encouragement and assistance given in the preparation of this monograph. I desire to acknowledge the cooperation and helpful criticism of Dr. L. R. Tehon of the Illinois State Natural History Survey, who has critically read the entire manuscript. Grateful acknowledgment is also made to Dr. John T. Buchholz, Professor of Botany in the University of Illinois, to Sister Mary Aquinas and Sister Mary Josephine of Rosary College, for their sympathetic insight and friendly suggestions, and to Miss Helen Checkowicz for her assistance in the preparation of the manuscript. I am also under obligation to Sister Mary Timothea who read the proof.

SISTER MARY HILAIRE RYAN, O.P.

Rosary College, River Forest, Illinois

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ALPHABETICAL LIST OF VALID GENERA

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Caenothyrium	27	Myiocopron	13
Calopeltis	16	Niesslella	22
Calothyriella	34	Parasterina	39
Calothyriopeltis	35	Peltella	15
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Caudella	35	Polythyrium	76
Chaetothyriopsis	16	Prillieuxina	77
Cirsosia	86	Ptychopeltis	83
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Clypeolella	46	Pycnopeltis	33
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Echidnodella	98	Seynesia	22
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Englera	45	Stegothyrium	35
Englerulaster	44	Stephanotheca	34
Halbania	27	Symphaster	100
Halbaniella	81	Thallochaete	73
Kriegeriella	81	Thyrosoma	33
Lembosia	87	Trichasterina	47
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Lembosiella	82		

INTRODUCTION

THE FIRST description of the family Microthyriaceae is given by Saccardo (46)* in 1886. It reads, "simple perithecia superficial, black, membranous to carbonaceous, dimidiate, flattened, context nearly always radiate." This description is entirely accurate, the characters easily recognizable and firmly established. Saccardo placed this family in the Dothideales. Von Höhnelt places it in the Perisporiales. Under the latter's leadership critical investigations have been undertaken resulting in a complete evolution in the taxonomy of the group. Chronologically the following five steps are noteworthy:

1913: Theissen and Sydow (76) created a new order, the Hemisphaeriales, for genera having a superficial, halbert to shield-shaped perithecium.

1915: Atkinson (7) considered the family represented reduced forms derived on the one hand from the Phacidiales, and on the other, perhaps, from the Sphaeriales. He did not definitely place it.

1918: Arnaud (1) said the family belonged to the Pyrenomycetes. He gave as his reason the fact that the asci are localized in particular zones formed by the gelatinization of the sterile cells of the cavity.

1920: Doidge (14), and Ryan (43) three years later, accepted Theissen and Sydow's classification in their taxonomic work.

1931: Clements and Shear (12) created the order Microthyriales.

Such differences as these indicate the development that has occurred since 1886.

This monograph is an effort to bring together the descriptions of genera and species, the record of the host plants, and the citations of original descriptions, so that future taxonomic work may be done more readily.

In preparing this work all data given in the publications listed in the bibliography have been utilized, as well as data from other periodicals in which only one or more species were described. Sources of these scattered data may be found in the citations following specific names of the individual species. They are not included in the bibliography.

*Numbers in parentheses following names of authors refer to items in the bibliography.

KEY TO GENERA

A. No free mycelium.....Subfamily Microthyreae Sacc. and Syd.

I. Hymenium simple:

a. Ascomata rounded:

1. Spores 1-celled, hyaline:

Paraphyses present..... 1. *Myiocopron*Paraphyses lacking..... 2. *Peltella*

2. Spores 2-celled:

(A) Spores hyaline:

Ascomata setose..... 3. *Chaetothyriopsis*

Ascomata glabrous:

Ascomata grown together..... 4. *Calopeltis*

Ascomata solitary:

Astomate..... 5. *Microthyriolum*

Stomate:

Ostiole a pore..... 6. *Microthyrium*Ostiole stellate..... 7. *Niesslella*

(B) Spores dark:

Ascomata smooth..... 8. *Seynesia*Ascomata setose..... 9. *Seynesiopeltis*

3. Spores 3- or 4-celled:

(A) Spores brown:

Cells approximately equal..... 10. *Scutellum*Midde cells larger..... 11. *Halbania*

(B) Spores hyaline:

Peristomal setae present..... 12. *Caenothyrium*

Setae lacking:

Scutellum dissolving..... 13. *Actinomyxa*

Scutellum persistent:

Not lichenicole..... 14. *Phragmothyrium*Lichenicole..... 15. *Micropeltopsis*

b. Ascomata linear:

1. Spores 2-celled:

(A) Spores hyaline:

Paraphyses present..... 16. *Lembosidium*Paraphyses lacking..... 17. *Aulographella*

(B) Spores dark:

Paraphyses present..... 18. *Lembosina*Paraphyses lacking..... 19. *Morenoina*

II. Several hymenia in each ascoma:

1. Spores 2-celled, hyaline:

Paraphyses lacking..... 20. *Thyrosoma*Paraphyses present..... 21. *Campoa*2. Spores many-celled, dark..... 22. *Pycnopeltis*

3. Spores muriform:

Asci single in peripheral zone..... 23. *Stephanotheca*Asci not in a peripheral zone..... 24. *Pycnoderma*

B. Free mycelium present, not membranous....Subfamily Asterineae Sacc. and Syd.

I. Hymenium simple:

a. Ascomata rounded:

1. Spores 1-celled:

(A) Spores hyaline:

Paraphyses present..... 25. *Calothyriella*Paraphyses lacking..... 26. *Stegothyrium*(B) Spores dark..... 27. *Calothyriopeltis*

2. Spores 2-celled:

(A) Spores hyaline:

Spores caudate, hyphopodia present..... 28. *Caudella*

Spores not caudate, hyphopodia lacking:

Ascomata setose..... 29. *Mycolangloisia*

Ascomata not setose:

Paraphyses present, not mucose..... 30. *Calothyrium*Paraphyses present, mucose..... 31. *Aphanopeltis*

(B) Spores dark:

Hyphopodia present:

Paraphyses present:

Ascomata not mucose-dissolving..... 32. *Parasterina*Ascomata mucose-dissolving..... 33. *Englerulaster*

Paraphyses lacking:

Ascomata mucose-diffuent..... 34. *Englera*

Ascomata not mucose-diffuent

Mycelial conidia 4-celled, astomate. 35. *Clypeolella*

Mycelial conidia not 4-celled:

Mycelium setose..... 36. *Trichasterina*Mycelium not setose..... 37. *Asterina*

Hyphopodia lacking:

Ascomata setose, mucose-encrusted:

Paraphyses lacking..... 38. *Asteromyxa*

Ascomata glabrous, not encrusted:

Mycelium setose..... 39. *Thallochaete*

Mycelium not setose:

Paraphyses present:

Paraphyses not gelatinous..... 40. *Asterinella*Paraphyses gelatinous..... 41. *Polythyrium*

Paraphyses lacking:

Conidia 4-celled..... 42. *Clypeolina*Conidia not 4-celled..... 43. *Prillieuxina*

3. Spores several-celled:

(A) Spores hyaline:

Paraphyses present..... 44. *Halbaniella*Paraphyses lacking..... 45. *Beelia*

(B) Spores dark:

Paraphyses lacking..... 46. *Kriegeriella*Paraphysate nodal cells present..... 47. *Platypeltella*4. Spores muriform, reddish..... 48. *Yatesula*

I. Hymenium simple (*continued*)

b. Ascomata linear:

1. Spores 1-celled, dark..... 49. *Lembosiella*

2. Spores 2-celled:

(A) Spores hyaline, hyphopodia none:

Paraphyses present:

Paraphyses simple..... 50. *Lembosiopsis*Paraphyses branched..... 51. *Ptychopeltis*Paraphyses lacking..... 52. *Aulographum*

(B) Spores dark:

Hyphopodia present:

Hyphopodia intercalary:

Paraphyses present..... 53. *Cirsosia*Paraphyses lacking..... 54. *Cirsosiella*

Hyphopodia not intercalary:

Paraphyses present..... 55. *Lembosia*Paraphyses lacking..... 56. *Morenoella*

Hyphopodia lacking:

Paraphyses present..... 57. *Echidnodes*Paraphyses lacking..... 58. *Echidnodella*

II. Hymenium with one ascus:

a. Spores 2-celled, dark..... 59. *Symphaster*

DESCRIPTION OF GENERA AND SPECIES

1. MYIOCOPRON Spegazzini

Fungi Arg., Pug. II, no. 142, Anal. Soc. Ci. Argentina 9:278-285. 1880.

Type: *M. corrientinum* Speg., *l. c.*

Characters: No free mycelium, ascomata thin, superficial, membranous or subcarbonous, dark, dimidate, radiate, smooth, circular, ostiolate. Hymenium simple, no epithecium. Asci many, 8-spored, clavate, thick-walled, paraphysate. Spores elliptical, continuous, hyaline.

Literature: Theissen and Sydow, 1917; Theissen, 1913; Saccardo, 1886, vol. 2, p. 659.

Figures: Saccardo, Genera Pyrenomycetes, tab. 12, fig. 16; Oudemans, Champ. Pays Bas, tab. 12, fig. 16, and Rev. Pyren. Batav., tab. 12, fig. 16.

Several species ascribed to the genus *Myiocopron* may belong to *Peltella*, as no mention of the presence or absence of paraphyses occurs in the original descriptions. Among these questionable species are: *M. dilatatum*, *M. cubense*, *M. granulatum*, *M. licatense*, *M. oleandri*, *M. baccharum*, *M. percirac*, *M. cucurbitaccarum*.

The species of *Myiocopron* are arranged in the order of maximum recorded spore length.

1. *Myiocopron lycopodii* Rostr., Beiheft. Bot. Centralbl. 3:3. 1896. On *Lycopodium*, Lycopodiales. Asci $25 \times 5 \mu$, spores $6 \times 1.5 \mu$. Syll. Fung. 11:379.

2. *Myiocopron baccharum* (Rehm) Sacc., Syll. Fung. 2:661. 1886. *Microthyrium baccharum* Rehm, Hedw. 21:122. 1882. On *Juniperus*, Pinaceae. Asci $30 \times 6 \mu$, spores $8 \times 2 \mu$.

3. *Myiocopron oleandri* (Pass.) Sacc., Syll. Fung. 2:659. 1886. *Microthyrium oleandri* Pass., Micr. Ital., no. 1, Rev. Myc. II, 1880. On *Nertium*, Apocynaceae. Asci $25 \times 12 \mu$, spores $7-9 \times 3-3\frac{1}{4} \mu$.

4. *Myiocopron litorale* Speg., Bol. Acad. Nac. Ci. Cordoba 25:88. 1921. On *Rhodostachys*, Bromeliaceae. Ascomata $150-180 \mu$, asci $75-80 \times 5-6 \mu$, spores $10 \times 2 \mu$.

5. *Myiocopron hederæ* (Feltg.) Stev., n. comb. *Phragmothyrium hederæ* v. Höhn., Ber. Deutsch. Botan. Ges. 37:111. 1919. *Mycrothyrium hederæ* Feltg., Vorstud. Pilzfl. Luxemb., Nachtr. 3:310. 1903. On *Hedera*, Araliaceae. Spores $10 \times 2.7-3.5 \mu$. Syll. Fung. 17:263. This species is removed from *Phragmothyrium* on account of its continuous spores.

6. *Myiocopron licatense* (Pass. and Beltr.) Sacc., Syll. Fung. 2:661.

1886. *Microthyrium licatense* Pass. and Beltr., Hedw. 22:111. 1883. On *Opuntia*, Cactaceae. Spores $10 \times 3 \mu$.

7. *Myiocopron stigmatostalycis* P. Henn., Hedw. 48:11. 1908. On *Stigmatostalycis*, Orchidaceae. Ascomata $250-300 \mu$, asci $45-60 \times 13-18 \mu$, spores $8-13 \times 4.5-5.5 \mu$. Syll. Fung. 24:422.

8. *Myiocopron cubense* (B. and C.) Sacc., Syll. Fung. 2:661. 1886. *Microthyrium cubense* Berk. and Curt., Cuban Fungi, no. 740, Jour. Linn. Soc. London, part 2, 1868. On *Dipteryce* (congo bean), Leguminosae. Spores $12-13 \times 6-7 \mu$.

9. *Myiocopron granulatum* (B. and Br.) Sacc., Syll. Fung. 2:659. 1886. *Micropeltis granulata* B. and Br., Fungi Ceylon no. 1139, Jour. Linn. Soc., part 2, 14. 1875. On *Caesalpinia*, Leguminosae. Spores $12-13 \times 7.5 \mu$.

10. *Myiocopron pereirae* F. Tassi, Bull. Lab. Ort. Bot., Siena, p. 142, tab. 11, fig. 4. 1899. On *Myroxydon*, Leguminosae. Ascomata 500μ , asci $50-60 \times 20 \mu$, spores $12-14 \times 8-10 \mu$. Syll. Fung. 16:634.

11. *Myiocopron ilicinum* (De Not.) Sacc., Syll. Fung. 2:660. 1886. *Microthyrium ilicinum* De Not., Erb. Cr. It., Ser. 1, n. 994, in Tassi, Fl. Sen. p. 61. 1862. On *Quercus*, Fagaceae. Spores 15μ long.

12. *Myiocopron pandani* v. Höhn., Ann. Myc. 17:115. 1919. On *Pandanus*, Pandanaceae. Ascomata $200-500 \mu$, often elongate, asci $26-30 \times 18-20 \mu$, spores $12-15 \times 5-8 \mu$. Syll. Fung. 24:422.

13. *Myiocopron corrientinum* Speg., Fungi Arg., Pug. II, no. 142. 1880. On *Oncidium*, Orchidiaceae. Ascomata $300-400 \mu$, asci $70 \times 20 \mu$, 8-spored, spores $13-16 \times 7-8 \mu$. Syll. Fung. 2:659.

14. *Myiocopron freycinetiae* (Stev. and Ryan) Arn., Ann. Crypt. Exot. 4:88. 1931. *Peltella freycinetiae* Stev. and Ryan, Bernice P. Bishop Mus. Bul. 19:69. 1925. On *Freycinetia*, Pandanaceae. Ascomata 280μ , asci $55-60 \times 29-26 \mu$, spores $5-7 \times 12-17 \mu$.

15. *Myiocopron palmarum* Wint., Hedw. 25:25. 1895. On *Palmae*. Ascomata $120-160 \mu$, asci $40-50 \times 23-26 \mu$, spores $16-17 \times 8-9 \mu$. Syll. Fung. 9:1053.

16. *Myiocopron umbilicatum* Speg., Bol. Acad. Nac. Ci. Cordoba 23:496. 1919. On *Bignoniaceae*. Ascomata $150-250 \mu$, asci $50 \times 30 \mu$, spores $18 \times 11 \mu$. Syll. Fung. 24:422.

17. *Myiocopron dilatatum* (B. and Br.) Sacc., Syll. Fung. 2:659. 1886. *Pamphidium dilatatum* B. and Br., Fungi Ceylon, no. 1134, Jour. Linn. Soc., part 2, 14. 1875. On *Palmae*. Spores $20 \times 15 \mu$.

18. *Myiocopron crustaceum* Speg., Fungi Guar., Pug. I, no. 293, Anal. Soc. Ci. Argentina 16. 1883. On *Palmae*. Ascomata $150-180 \mu$, asci $40-50 \times 15-20 \mu$, spores $15-20 \times 7-8 \mu$. Syll. Fung. 9:1053; Ann. École Nac. Agr. Montp. 18:199. 1920.

19. *Myiocopron yerbae* Speg., Ann. Mus. Nac. Buenos Aires, Ser. 3, 10:130. 1909. On *Ilex*, Aquifoliaceae. Ascomata 75-100 μ , asci 60-70 x 25-30 μ , spores 26-28 x 12-14 μ . Syll. Fung. 22:514.

20. *Myiocopron caseariae* Speg., Ann. Mus. Nac. Buenos Aires 23:79. 1912. On *Casearia*, Flacourtiaceae. Ascomata 350-500 μ , asci 80 x 15-18 μ , spores 25-30 x 5-6 μ . Syll. Fung. 24:422.

21. *Myiocopron ramulare* (Ell.) Speg., Ann. Myc. 10:194. 1912. *Asterina ramularis* Ell., Bull. Torr. Bot. Club 9:20. 1882. On *Laurus*, Lauraceae. Syll. Fung. 16:634.

22. *Myiocopron cucurbitacearum* Rehm, Hedw. 39:226. 1900. On Cucurbitaceae. Ascomata 1-1½ mm., asci 20 x 8-9 μ . Syll. Fung. 16:634.

2. PELTELLA Sydow

Annales Mycologici 15:237. 1917.

Type: *P. conjuncta* Syd.

Characters: Ascomata superficial, dimidiate, inverse-radiate, often confluent. No free mycelium. Asci ovate, 8-spored, paraphysate. Spores 1-celled, hyaline. *Actinothyrium* appears to be a conidial stage. The basis for the separation of this genus from *Myiocopron* is the absence of paraphyses, though Sydow described the type species as "mucose paraphysate."

Literature: Theissen, 1913; Saccardo, 1926.

1. *Peltella validivianum* (Speg.) Stev., n. comb. *Myiocopron validivianum* Speg., Fungi Chilensis 103. 1910. On *Eugenia*, Myrtaceae. Ascomata 75-90 μ , asci 27-30 x 6 μ , spores 8 x 2 μ . Syll. Fung. 22:514.

2. *Peltella insignis* Toro, Jour. Dept. Agr. Puerto Rico 13:233. 1930. On *Bromelia*, Bromeliaceae. Ascomata 100-120 μ , asci 42-49 x 13-15 μ , spores 10-12 x 5-6 μ .

3. *Peltella argentinense* (Speg.) Stev., n. comb. *Myiocopron argentinense* Speg., Ann. Mus. Nac. Buenos Aires 12:423. 1909. On *Foeniculum*, Umbelliferae. Ascomata 120 μ , asci 50 x 9-10 μ , spores 14-15 x 3-3½ μ . Syll. Fung. 22:515.

4. *Peltella conjuncta* (H. and P. Syd.) Syd., Ann. Myc. 15:237. 1917. *Myiocopron conjunctum* H. and P. Syd., Ann. Myc. 12:200. 1914. On *Daemonorops* and *Calamus*, Palmae. Ascomata 100-160 μ , asci 28-32 x 20-25 μ , spores 14-17 x 7-8 μ . Syll. Fung. 24:423.

5. *Peltella millepunctata* (Penz. and Sacc.) Stev., n. comb. *Myiocopron millepunctatum* Penz. and Sacc., Malpighia 11:524. 1897. On *Psilotum*, Pteridophyta. Ascomata 300 μ , asci 45-50 x 15 μ , spores 18 x 6-7 μ . Syll. Fung. 14:687.

6. **Peltella bakeriana** (Rehm) Stev., n. comb. *Myiocopron bakerianum* Rehm, Philipp. Jour. Sci. c. Bot. 8:393. 1913. On Passiflora, Passifloraceae. Ascomata 250-300 μ , asci 50 x 10-12 μ , spores 12-15 x 5 μ .

7. **Peltella affine** (Penz. and Sacc.) Stev., n. comb. *Myiocopron affine* Penz. and Sacc., Malpighia 11:525. 1897. On Monocotyledons. Ascomata 330-350 μ , asci 45-50 x 18-22 μ , spores 15 x 7 μ . Icones F. Jav. tab. 40, fig. 4. Syll. Fung. 14:1899.

8. **Peltella vaccinii** (De Not.) Stev., n. comb. *Myiocopron vaccinii* Sacc., Syll. Fung. 2:660. 1886. *Microthyrium vaccinii* De Not., Micr. Ital., Dec. 4, p. 22, fig. 4. 1842. On Vaccinium, Ericaceae. No measurements given.

9. **Peltella smilacis** (De Not.) Stev., n. comb. *Myiocopron smilacis* Sacc., Ann. Myc. 7:414. 1909. *Microthyrium smilacis* De Not., Micr. Ital., Dec. 4, p. 22, fig. 4. 1842. On Smilax, Liliaceae; Alpinia, Zingiberaceae. Asci 60-62 x 20 μ , spores 10 x 6 μ . Syll. Fung. 2:660. 1886.

3. CHAETOTHYRIOPSIS Stevens and Dorman

Mycologia 19:237. 1927.

Type: *C. panamensis* Stev. and Dorm.

Characters: Thallus radiate, superficial, no free mycelium. Ascomata setose, single, ostiolate, round. Spores 1-septate, hyaline, apapophysate.

1. *Chaetothyriopsis panamensis* Stev. and Dorm., l. c. On Oncoba, Flacourtiaceae. Ascomata 40-70 μ , asci 21-22 x 7 μ , spores hyaline, 2-celled 7 x 2 μ , setae 3-4, simple, septate, arising from margin of ostiole, 36-70 μ long.

4. CALOPELTIS Sydow

Annales Mycologici 23:392. 1925.

Type: *C. acnisti* Syd.

Characters: Like *Microthyrium* but ascomata grown together.

1. *Calopeltis acnisti* Syd., l. c. On Acnistus, Solanaceae. Ascomata 100-180 μ , asci 45-60 x 13-19 μ , spores 13-19 x 5-8 μ .

2. *Calopeltis tetraspora* Toro, Ann. Myc. 32:110. 1934. On Symplocus, Symplocaceae. Ascomata 143-291 x 131-285 μ , asci 40-45 x 9-12 μ , spores 14-19 x 2-3 μ .

5. MICROTHYRIOLUM Spegazzini

Bol. Acad. Nac. Ci. Cordoba 23:497. 1919.

Type: *M. apiahynum* Speg.

Characters: No free mycelium, ascomata round, astomate, glabrous, stellate, dehiscent, spores 2-celled, hyaline, pseudoparaphyses few.

This genus differs from *Microthyrium* in being astomate.

1. *Microthyriolum apiahynum* Speg., l. c. *Microthyrium apiahynum* Speg., Fungi Chilensis, p. 104. 1910. On *Persea*, Lauraceae. Ascomata 100-150 μ , asci 50 x 30 μ . Syll. Fung. 9:1055.

2. *Microthyriolum* (?) *obligosporum* Speg., Bol. Acad. Nac. Ci. Cordoba 23:499. 1919. On Solanaceae (?). Ascomata 150-200 μ , asci 50-60 x 40 μ , spores 30 x 12-15 μ . Syll. Fung. 22:442.

3. *Microthyriolum astomum* (Speg.) Speg., Bol. Acad. Nac. Ci. Cordoba 23:499. 1919. *Microthyrium* (?) *astomum* Speg., Fungi Chilensis, p. 104. 1910. On *Cryptocarya*, Lauraceae. Ascomata 50-60 μ , asci 30 x 14 μ , spores 10 x 3 μ . Syll. Fung. 22:518.

4. *Microthyriolum subimperspicuum* Speg., Ann. Mus. Nac. Buenos Aires 31:423. 1923. On *Pithecolobium*, Leguminosae. Ascomata 80-100 μ , asci 50-60 x 15-20 μ , spores 20 x 4 μ .

6. MICROTHYRIUM Desmazières

Annales des Sciences Naturelles 15:138. 1841.

Type: *M. microscopicum* Desm.

Characters: Ascomata superficial, dimidiate, ostiolate, aparaphysate, spores 1-septate, hyaline.

The original description reads "aparaphysate," as does that of the type species, yet Theissen and Sydow say, "wie Myiocopron, Sporen farblos, zweizellig," and they give *Myiocopron* as paraphysate. As a matter of fact 10 species are described as paraphysate, while in 17 there is no mention made of paraphyses.

Nos. 1-10, paraphysate.

Nos. 11-30, aparaphysate.

Nos. 31-49, paraphyses not recorded; probably there are none.

Nos. 9, 43, and 48 are questionable species.

Literature: Theissen, 1912 and 1913; Saccardo, 1886, vol. 2, p. 662.

Figures: Saccardo, Genera Pyrenomycetes, tab. 12, fig. 19; Oudemans, Champ. Pays Bas, tab. 12, fig. 19, and Rev. Pyren. Batav., tab. 12, fig. 19.

1. *Microthyrium paraguayense* Speg., Fungi Guar., Pug. I, no. 294, Anal. Soc. Ci. Argentina 16. 1883. On Sapindaceae. Ascomata 140-180 μ , asci 30-32 x 8-10 μ , spores 8 x 3 μ , paraphysate. Syll. Fung. 9:1055. 1891.

2. *Microthyrium ekmanii* Petr. and Cif., Ann. Myc. 30:206. 1932. On *Ocotea*, Lauraceae. Ascomata 150-250 μ , asci 45-65 x 15-23 μ , spores 5.5-8.5 x 5-7 μ , paraphysate.

3. *Microthyrium exarescens* Rehm, Hedw. 39:227, fig. 2. 1900. On leaves. Ascomata 200-300 μ , asci 35-40 x 12-14 μ , spores 10-12 x 3 μ , paraphysate.

4. *Microthyrium calophylli* Ryan, Mycologia 16:179. 1924. On *Calophyllum*, Guttiferae. Ascomata 224-336 μ , asci 9.6 x 62 μ , spores 10-12 x 3 μ , paraphysate.
5. *Microthyrium laurenti* P. Henn., Mission E. Laurent, fasc. 3:317. 1906. On *Coffea*, Rubiaceae. Ascomata 130-160 μ , asci 25-35 x 8-11 μ , spores 10-14 x 3.5-4.5 μ , paraphysate. Syll. Fung. 22:519. 1913.
6. *Microthyrium epimyces* Sacc., Bomm., and Rouss., Fl. Myc. Belg. 2:23. Rehm, Ascom. no. 899. On *Prunus*, Rosaceae. Ascomata 130 μ , asci 36-42 x 15 μ , spores 18 x 6 μ , paraphysate. Syll. Fung. 9:1060. 1891.
7. *Microthyrium ranulisporum* Doidge, Bothalia 1:65. 1921. On *Scolopia*, Flacourtiaceae. Ascomata 240-360 μ , asci. 90-100 x 10-14 μ , spores 6.5-8.5 x 3.5-5 μ , paraphysate.
8. *Microthyrium malacoderma* (v. Höhn.) Sacc. and Trott., Syll. Fung. 22:217. 1913. *Microthyriella malacoderma* v. Höhn., Sitz. K. Akad. Wiss. Wien, Math.-Nat. Kl. Abt. I, 118:1173. 1909. On *Paratropsis*, Araliaceae. Ascomata 1000 μ , asci 120-140 x 80-85 μ , spores 85-110 x 18-24 μ , paraphyses present.
9. *Microthyrium harrimani* Sacc., Harrim. Alaska Exped., Crypt., p. 26, pl. 2, fig. 1. 1904. On *Tsuga*, Pinaceae. Ascomata 350-450 μ , asci 80-100 x 9-10 μ , paraphysate. Questionable species. Syll. Fung. 17:864.
10. *Microthyrium mischocarpi* Syd., Ann. Myc. 15:238. 1917. On *Mischocarpus*, Sapindaceae. Ascomata 140-170 μ , asci 36-48 x 14-16 μ , spores 12-14 x 3-3.5 μ , Syll. Fung. 2:426.
11. *Microthyrium antarcticum* Speg., Fungi Feug. no. 280. Bol. Acad. Nac. Ci. Cordoba 11:238. 1889. On *Berberis*, Berberidaceae. Ascomata 100-140 μ , asci 22-27 x 3.5-4.5 μ , spores 7-8 x 2-3 μ , paraphysate. Syll. Fung. 9:1056.
12. *Microthyrium cytisti* Fckl., Symb. Myc., p. 98. 1869-70. Saccardo, Reliq. Lib. 2, no. 140, tab. 19, fig. 7. *Microthyrium genistae* Niessl. On *Cytisus*, Leguminosae. Ascomata 120 μ , asci 30 x 6-7 μ , spores fusoid, 7-8 x 2.5 μ , paraphysate. Rev. Myc. 3, tab. 19, fig. 7. 1881. Syll. Fung. 2:663.
13. *Microthyrium alpestre* Sacc., Michelia 2:160. 1882. On *Carex*, Cyperaceae. Ascomata 100-130 μ , asci 28-30 x 6 μ , spores 10-12 x 3-4 μ , paraphysate. Syll. Fung. 2:666.
14. *Microthyrium styracis* Starb., Arkiv. Botan. 2:12. 1904. On *Styrax*, Styracaceae. Ascomata 100-120 μ , asci 31-38 x 5.5-7.5 μ , spores 11-12 x 4.5-5 μ , paraphysate. Syll. Fung. 17:262.
15. *Microthyrium xylogenum* Bomm., Rouss., and Sacc., Attid. R. Istit. Veneto di Sci. 1884. On *Fagus*, Fagaceae. Ascomata 100-120 μ , asci 36 x 8-9 μ , spores 11-13 x 2-2.5 μ , paraphysate. Syll. Fung. 9:1059.
16. *Microthyrium eucalypticola* Speg., Ann. Mus. Nac. Buenos Aires

12:426. 1909. On Eucalyptus, Myrtaceae. Ascomata 150 μ , asci 30-40 x 8-9 μ , spores 12-14 x 3 μ , paraphysate.

17. *Microthyrium culmigenum* Syd., Ann. Myc. 19:140. 1921. On Calamagrostis, Gramineae. Ascomata 150-180 μ , asci 35-48 x 8-10 μ , spores 10-15 x 3-3.5 μ , paraphysate.

18. *Microthyrium litigiosum* Sacc., Fungi Ital., fig. 564; *Michelia* 1:496. 1877. On Pteris, Pteridophytes. Ascomata 170 x 150 or 200-300 x 110-170 μ , asci 20-25 x 12-14 μ , spores curved, 15 x 2-3 μ , paraphysate. Syll. Fung. 2:664.

19. *Microthyrium virescens* Speg., Fungi Puigg. no. 336, Bol. Acad. Nac. Ci. Cordoba 11:553. 1889. On Eugenia, Myrtaceae. Ascomata 80-100 μ , asci 36-42 x 18-24 μ , spores 13-16 x 5-6 μ , paraphysate. Syll. Fung. 9:1056.

20. *Microthyrium melastomacearum* Speg., Fungi Puigg. no. 335, Bol. Acad. Nac. Ci. Cordoba 11:553. 1889. On Melastomaceae. Ascomata 150-250 μ , asci 52-75 x 10-13 μ , spores 14-16 x 4-5 μ , paraphysate. Hedw. 37:327. fig. 2. 1898. Syll. Fung. 9:1056.

21. *Microthyrium vittiforme* Speg., Fungi Arg. novi v. crit., p. 297. 1899. On Scirpus, Cyperaceae. Ascomata 60 x 100 μ , asci 22-30 x 18-25 μ , spores 14-16 x 4-5 μ , paraphysate. Syll. Fung. 16:636.

22. *Microthyrium microscopicum* Desm., Ann. Sci. Nat. 15:138, tab. 14, fig. 1. 1841. On Buxus, Buxaceae; Quercus and Fagus, Fagaceae; Vinca, Apocynaceae; Rhus, Anacardiaceae; Symphoricarpos, Caprifoliaceae; Dacrydium, Taxaceae. Ascomata 150 μ , asci 25-30 x 7-9 μ , spores 8-10 x 3-3.5 μ , paraphysate.

Var. microspora. Asci 45-50 x 10 μ , spores 15-17 x 4 μ .

Var. major Speg., Fungi Chilensis, p. 105. 1910. On Persea, Lauraceae. Ascomata 100-150 μ , asci 45 x 8-9 μ , spores 12-14 x 4-5 μ , paraphysate. Syll. Fung. 22:518.

Var. minor Speg., Fungi Chilensis, p. 105. 1910. On Persea linguae, Lauraceae. Ascomata 100 μ , asci 35-40 x 8 μ , spores 10-11 x 4 μ . Cooke, Handb. 2, p. 927, f. 402; Corda, Anleit., tab. F, fig. 52, 17-20; Lindau in Engler, Pflanzenfam. 1, 1, 341, fig. 234 B-D; Neger in Kryptog. Flora Brandenb., 7, p. 138, fig. 6; Saccardo, Fungi Ital., fig. 562; Winter, Kryptog. Flora, 2, p. 52. Syll. Fung. 2:662.

23. *Microthyrium litorale* Speg., Bol. Acad. Nac. Ci. Cordoba 25:89. 1921. On Rhodostachys, Bromeliaceae. Ascomata 150-200 μ , asci 50 x 14 μ , spores 18 x 6-8 μ , paraphysate.

24. *Microthyrium thyriascum* Schulze and Sacc., Micr. Slav. no. 5, Rev. Myc. 6:71. 1884. On Quercus, Fagaceae. Ascomata 250-300 μ , asci 60 x 30 μ , spores 19 x 10 μ , paraphysate. Syll. Fung. 9:1057.

25. *Microthyrium fuscillum* Sacc., *Michelia* 2:57. 1882. On Teu-

crium, Labiatae. Ascomata $150\ \mu$, asci $60-70 \times 20\ \mu$, spores $23-25 \times 7-8\ \mu$, paraphysate. Syll. Fung. 2:665.

26. *Microthyrium annuliforme* Syd., Ann. Myc. 12:488. 1914. *Microthyrium maculicolum* Doidge, Trans. Roy. Soc. So. Afr. 8:241. 1920. On Capparis (?), Capparidaceae. Ascomata $100-140\ \mu$, asci $35-45 \times 30-35\ \mu$, spores $18-23 \times 7-10\ \mu$, paraphysate. Measurements given by Doidge are: ascomata $160-190\ \mu$, asci $70 \times 27\ \mu$, or $50-57 \times 30-43\ \mu$, spores $21-23 \times 6.5-10\ \mu$.

27. *Microthyrium confusum* (Desm.) v. Höhn., Ber. Deutsch. Botan. Ges. 37:111. 1919. *Microthyrium microscopicum* Desm. var. *confusum* Desm. No paraphyses present.

28. *Microthyrium loranthei* (Karst and Hariot) Theiss., Ann. Myc. 14:270. 1916. *Hariotula loranthei* Arn., Ann. École Nac. Agr. Montp., nov. ser., 16:201. 1918. *Clypeolum loranthei* Karst. and Hariot, Asco. nov., Rev. Myc. 12:173. 1890. On Loranthus, Loranthaceae. Ascomata $160-200\ \mu$, asci $56 \times 16\ \mu$, or $82 \times 11-13\ \mu$, spores $20-22 \times 6\ \mu$, paraphysate.

29. *Microthyrium senegalense* Speg., Ann. Mus. Nac. Buenos Aires 26:128. 1914. On Penicellaria, Gramineae. Ascomata $150-300\ \mu$, asci $30 \times 10\ \mu$, spores $9 \times 3\ \mu$, paraphysate. Syll. Fung. 24:424.

30. *Microthyrium scutiae* Speg., Ann. Mus. Nac. Buenos Aires 23:79. 1912. On Scutia, Rhamnaceae. Ascomata $150-200\ \mu$, asci $20-25 \times 5-6\ \mu$, spores $8 \times 1.5\ \mu$, paraphysate. Syll. Fung. 24:426.

31. *Microthyrium acervatum* Speg., Fungi Guar., Anal. Soc. Ci. Argentina 26:40. 1888. On Rutaceae; Cayaponia, Cucurbitaceae. Ascomata $45-58\ \mu$, asci $28-32 \times 17-18\ \mu$, spores $12 \times 4.5\ \mu$, paraphyses (?). Hedw. 39:299, fig. 1. 1900. Syll. Fung. 11:380. 1895.

32. *Microthyrium mauritanicum* Dur. and Mont., Fl. Alg. I, p. 615. 1849. On Arundo, Gramineae. Ascomata $100\ \mu$, asci $19 \times 13\ \mu$, spores $12 \times 3\ \mu$, paraphyses (?). Baccarini and Avetta, Ann. Inst. Bot. Roma, 1885, tab. 16, fig. 6. Syll. Fung. 2:664; 9:1058. 1891.

33. *Microthyrium michelianum* Togn., Atti. Ist. Bot. Pavia 5:7, tab. 1, fig. 16-19. 1899. On Castanea, Fagaceae. Ascomata $200\ \mu$, asci $60 \times 13-15\ \mu$, spores $13 \times 5-6\ \mu$, paraphyses (?). Syll. Fung. 11:380.

34. *Microthyrium angelicae* Fautr. and Roum., Rev. Myc. 14:8. 1892. On Angelica, Umbelliferae. Asci $14-20 \times 14\ \mu$, spores $10-14 \times 4-5\ \mu$, paraphyses (?). Syll. Fung. 11:379. 1895.

35. *Microthyrium amygdalinum* Cooke and Mass., Grev. 19:90. 1890. On Eucalyptus, Myrtaceae. Spores ellipsoid, $14 \times 7\ \mu$, paraphyses (?). Cooke, Austr. Fung., tab. 25, fig. 237. Syll. Fung. 9:1057.

36. *Microthyrium mangiferae* Bomm. and Rouss., Bol. Soc. Roy. Bot. Belg. 35:164. 1896. On Mangifera, Anacardiaceae. Ascomata $140-180\ \mu$, asci 108×18 or $46 \times 21\ \mu$, spores $14 \times 6\ \mu$, paraphyses (?). Syll. Fung. 14:687.

37. *Microthyrium gomphisorum* (B. and Br.)¹ Sacc., Syll. Fung. 2:665. 1886. *Micropeltis gomphispora* (Berk. and Broome) Berk., Jour. Linn. Soc. 14:132, tab. 9, fig. 48. 1874. Spores cuneiform, 8-15 μ , paraphyses (?).

38. *Microthyrium abietis* Mont., Not. Ascom. p. 79. On *Abies*, Pinaceae. Ascomata 200 μ , asci 40 x 13 μ , spores 17 x 5 μ , paraphyses (?). Syll. Fung. 9:1058. 1891. Ann. Myc. 22:263. 1924.

39. *Microthyrium boivini* Mont., Ann. Sci. Nat., 4 sér., 7:134. 1857. On leaves. Ascomata 1-3 mm., asci 50 μ , spores 30 x 10 μ , paraphyses (?). Syll. Fung. 2:665.

40. *Microthyrium phegopteridis* P. Magn., Abh. Naturh. Ges. Nurnb. 16:74. 1906. On *Phegopteris*, Pteridophyta. Ascomata 78-140 μ , paraphyses (?). Syll. Fung. 22:520.

41. *Microthyrium millettiae* Smith, Jour. Bot. 36:179. 1898. On *Millettia griffoniana*, Leguminosae. Ascomata 500 μ , asci 55-35 μ , spores 35-40 μ x 10-12 μ , paraphyses (?). Syll. Fung. 16:635.

42. *Microthyrium macrosporum* (Sacc.) v. Höhn., Ber. Deutsch. Bot. Ges. 37:110. 1919. *Microthyrium microscopicum* Des. v. *macrospora* Sacc., Syll. Fung. 2:662. 1886. On *Buxus*, Buxaceae. Ascomata 150 μ , asci 45-50 x 10 μ , spores 15-17 x 4 μ .

43. *Microthyrium erysiphoides* (E. and M.), Theiss. Abh. K. K. Zool.-Bot. Ges. 7:25. 1913, is a *Microthyrium* or a *Microthyriella*. *Asterina patelloides* E. and M., Jour. Myc. 1:136. 1885. *Asterina erysiphoides* E. and M. (not K. and C.), N. A. F. no. 13591. *Asterella erysiphoides* Sacc., Syll. Fung. 9:394. 1891. N. A. F. no. 1359. On *Quercus*, Fagaceae. Ascomata 275-300 μ , asci 36 x 15 μ , spores 15 x 6 μ , paraphyses (?). Ann. Myc. 10:199. 1912.

44. *Microthyrium punctiforme* (Berk. and Curtis) Sacc., Syll. Fung. 2:665. 1886. *Micropeltis punctiformis* B. and C., Cuban Fungi no. 744, Jour. Linn. Soc. 10:1868. On leaves. Spores 15 x 2.5-3 μ , paraphyses (?).

45. *Microthyrium psychotriae* Masee, Jour. Bot. 34:152. 1896. On *Psychotria*, Rubiaceae. Ascomata 100-125 μ , asci 45-50 x 6-7 μ , spores clavate, 7-8 x 3-2 μ , paraphyses (?). Syll. Fung. 14:688.

46. *Microthyrium graminum* Bomm., Rouss., and Sacc., Syll. Fung. 9:1059. 1891. *Var.* major Grove, Jour. Bot. 71:286. 1933. On *Psamma*, Gramineae. Ascomata 70-90 μ , asci 27-30 x 7.5-10 μ , spores 9 x 3 μ , paraphyses (?).

47. *Microthyrium corynellum* Tassi, Bull. Lab. Ort. Bot., Siena, 10:97, fig. 2. 1900. On *Leptospermum*, Myrtaceae. Ascomata 100-140 μ , asci 35-40 x 6-8 μ , spores 8-10 x 2 μ , paraphyses (?). Syll. Fung. 16:635.

48. *Microthyrium arcticum* Oudem., Contr. Flore Myc. Nowaja Semlja, p. 15, tab. 1, fig. 16. 1885. On *Potentilla*, Rosaceae. Ascomata 60-100 μ , asci 35 x 7 μ . A doubtful species. Syll. Fung. 9:1038. 1891.

49. *Microthyrium platani* Rich., Syll. Fung. 9:1061. 1891. On *Platanus*, *Platanaceae*. Ascomata 100-130 μ , asci 40-48 x 5-7 μ , spores 8-10 x 2.5-3.5 μ .

50. *Microthyrium rhododendri* Grove, Jour. Bot. 71:287. 1933. On *Rhododendron*, *Ericaceae*. Ascomata 400 x 200 μ , asci 35-40 x 20-25 μ , spores 20 x 9-10 μ , paraphyses not seen.

7. NIESSLELLA v. Höhnelt

Ber. Deutsche Botanische Gesellschaft 36:468. 1918.

Type: *N. scirpicola* (Fckl.) v. Höhn.

Characters: Free mycelium none, ascomata radiate, ostiole, at first lacerate then broadly round, simulating the *Discomycetes*. Excipulum present or absent. Paraphyses filiform, simple. Asci clavate, 8-spored, spores elongate, hyaline, 2 (or 4?) celled.

1. *Niesslella scirpicola* (Fckl.) v. Höhn., l. c. *Micropeziza scirpicola* Fckl. 1869. *Mollisia scirpicolum* (Fckl.) Sacc. 1889. *Belonidium scirpicolum* (Fckl.) Rehm, 1891. On *Scirpus*, *Cyperaceae*. Asci 54 x 8 μ , spores 12-14 x 3 μ . Syll. Fung. 8:348.

2. *Niesslella aurantiaca* (Rehm) v. Höhn., l. c. *Belonidium aurantiacum* Rehm, Disco. p. 564. 1891. On *Carex*, *Cyperaceae*. Asci 60-70 x 8 μ , spores 1-3 septate, hyaline, 10-15 x 1.5 μ , paraphysate. Syll. Fung. 24:533, 10:29.

8. SEYNESIA Saccardo

Sylloge Fungorum 2:668. 1886.

Type: *S. nobilis* (Welw. and Curr.) Sacc.

Characters: No free mycelium, ascomata circular, radiate, ostiolate, spores dark, 2-celled. Like *Microthyrium* but with brown spores.

Literature: Öst. Bot. Zeitschr. 63:121-131. 1913. Atti dell' Acad. Ven.-Trent. 10:61. 1917.

Synonymous genera:

1) *Arnaudiella* Petr., Ann. Myc. 25:339. 1927. Type: *A. caronae* (Pass.) Petr.,—*Seynesia caronae* Pass.,—*Seynesia pulchella* Bomm., Rouss., and Sacc. The many dimidiate forms formerly placed in *Arnaudiella* according to Petrak must find place in *Seynesia*.

2) *Seynesiola* Speg., Bol. Acad. Nac. Ci. Cordoba 23:498. 1919. Type: *S. chilensis* Speg. There is no sufficient distinction from *Seynesia*.

3) *Ferrarisia* Sacc., Atti dell' Acad. Ven.-Trent. 3:10-61. 1919; emend. Petr., Ann. Myc. 25:343. 1927. Type: *F. ipomoeae* (Syd.) Petr.,—*Seynesia ipomoeae* Syd.,—*Ferrarisia philippina* Sacc. This genus may be united with *Seynesia*.

4) *Seynesiella Arn.*, Ann. École Nac. Agr. Montp. 16:202. 1918. Type: *S. juniperi* (Desm.) Arn., Syll. Fung. 24:502. May be united with *Seynesia*.

1. *Seynesia cordiae* Ryan, Mycologia 16:178. 1924. On *Cordia*, Boraginaceae. Ascomata 150-240 μ , asci 17 x 34 μ , spores 10 x 3.5 μ , paraphysate.

2. *Seynesia eugeniae* (Syd.) Stev., n. comb. *Ferrarisia eugeniae* Syd., Ann. Myc. 27:66. 1929. On *Eugenia*, Myrtaceae. Ascomata 60-100 μ , asci 16-23 x 14-17 μ , spores 8-11 μ , paraphysate.

3. *Seynesia coccolobae* Ryan, Mycologia 16:178. 1924. On *Coccoloba*, Polygonaceae. Ascomata 672-1200 μ , asci 19-21 x 84-96 μ , spores 19 x 7-8 μ .

4. *Seynesia brasiliensis* Speg., Rev. Mus. La Plata 15:29. 1896. On leaves. Ascomata 250 μ , asci 80-100 x 20-25 μ , spores 24-25 x 12 μ , paraphysate. Syll. Fung. 22:524. 1913.

5. *Seynesia alstoniae* Rehm, Leaflets Philipp. Bot. 6:2227. 1914. Asco. exs. 2164. On *Alstonia*, Apocynaceae. Ascomata 500-1000 μ , asci 50-70 x 30-40 μ , spores 27-30 x 12-14 μ , paraphysate. Syll. Fung. 24:427; v. Höhnelt, Ann. Myc. 16:221. 1918.

6. *Seynesia fusco-paraphysata* Henn., Engl. Bot. Jahrb. 33:48. 1903. On *Tabernaemontana*, Apocynaceae. Ascomata 1000-1500 μ , asci 80-90 x 28-32 μ , spores 32-36 x 10-13 μ , paraphysate. Syll. Fung. 17:867; Öst. Bot. Zeitschr. 63:125. 1913.

7. *Seynesia melanosticta* Cooke and Mass., Grev. 18:34. 1889. On *Alsodeia*, Violaceae. Ascomata 500 μ , spores 10 x 3-5 μ , paraphyses (?). Syll. Fung. 9:1066.

8. *Seynesia echitis* (Allesch.) Theiss., Beiheft. Bot. Centralbl. Abt. II. 29:53. 1912. *Dimerosporium echitis* Allesch., Hedw. 36:235. 1897. On *Echites*, Apocynaceae. Ascomata 80-140 μ , asci 30-35 x 20 μ , spores 10 x 5 μ , paraphyses (?). Syll. Fung. 14:468; Öst. Bot. Zeitschr. 63:127. 1913.

9. *Seynesia montana* (Rac.) Sacc. and Trott., Syll. Fung. 22:524. 1913. *Trichopeltis montana* Rac., Bul. Acad. Sci. Cracovie, p. 378. 1909. On *Vaccinium*, Ericaceae. Ascomata 170-220 μ , asci 36-50 x 8-10 μ , spores 11-14 x 3-4 μ , paraphyses (?).

10. *Seynesia pontica* (Bub.) Theiss., Abh. K. K. Zool.-Bot. Ges. 7:33. 1913. *Asterina pontica* Bub., Handel-Mazzetti Bot. Pont. Randyeb. Ann. Naturhist. Hofmus. Wien 23:102, tab. 5, fig. 1, a-f. 1909. On *Daphne*, Thymelaceae. Ascomata 200-400 μ , asci 30-45 x 22-25 μ , spores 12-15 x 4-4.5 μ , paraphyses (?). Syll. Fung. 22:541.

11. *Seynesia ipomoeae* Syd., Philipp. Jour. Sci. 8:488. 1913. *Ferrarisia philippina* Sacc., Atti dell' Acad. Ven.-Trent. Notae Mycol. 23. 1917. *Ferrarisia ipomoeae* (Syd.) Petr., Ann. Myc. 25:343. 1927. On

Ipomoea, Convolvulaceae. Ascomata 500-1500 μ , asci 30-35 x 24-28 μ , spores 15-17 x 7.5-8.5 μ , paraphysate. Syll. Fung. 24:428; Ann. Myc. 29:223. 1931.

12. *Seynesia orbiculata* H. and P. Syd., Ann. Myc. 10:39. 1912. On *Euclea*, Ebenaceae. Ascomata 90-175 μ , asci 35-60 x 16-25 μ , spores 13-18 x 6-8 μ , paraphyses (?). Syll. Fung. 24:428; Trans. Roy. Soc. So. Afr. 8:242. 1920.

13. *Seynesia microthyriodes* (Wint.) Theiss., Öst. Bot. Zeitschr. 63:125. 1913. *Asterina microthyrioides* Wint., Hedw. 25:94. 1885. *Asterina solanicola* Kalch. and Cke., (not Berk. and Curtis), Grev. 9. 1880. *Asterina erysiphoides* Kalch. and Cke., Grev. 9. 1880. On *Eucalyptus*, Myrtaceae. Ascomata 300 μ , asci 40-50 x 18-21 μ , spores 19 x 5 μ , paraphyses (?). Syll. Fung. 9:380. 1891.

14. *Seynesia costaricensis* Speg., Acad. Nac. Ci. Cordoba, Bol. 23:570. 1919. On *Gaulthera*, Ericaceae. Ascomata 90-120 μ , asci 38-45 x 30 μ , spores 20 x 6-7 μ , paraphyses (?). Syll. Fung. 24:428.

15. *Seynesia drymidis* (Lév.) Speg., Fungi Chilensis 108. 1910. On *Drymis*, Magnoliaceae. Ascomata 120-150 μ , asci 42-50 x 28-30 μ , spores 20-23 x 9-10 μ , paraphyses (?).

16. *Seynesia ficina* Syd., Ann. Myc. 14:365. 1916. On *Ficus*, Moraceae. Ascomata 220-300 μ , asci 45-55 x 35-40 μ , spores 22-23 x 10-14 μ , paraphyses (?). Syll. Fung. 24:429.

17. *Seynesia calamicola* P. Henn. and Nym., Monsunia 1:160. 1899. On *Calamus*, Palmae. Ascomata 500-600 μ , spores 24-27 x 9-10 μ , paraphyses (?). Syll. Fung. 16:641; Öst. Bot. Zeitschr. 63:124. 1913.

18. *Seynesia nobilis* (Welw. and Curr.), Sacc., Syll. Fung. 2:668. 1886. *Pemphidium nobile* Welw. and Curr., Fungi Angol., Trans. Linn. Soc. London 26:283, tab. 17, fig. 12. 1867. On *Elais*, Palmae. Spores 25-28 μ , paraphyses (?). Öst. Bot. Zeitschr. 63:125. 1913.

19. *Seynesia apuleiae* Speg., Ann. Mus. Nac. Buenos Aires 23:80. 1912. On *Apuleia*, Leguminosae. Ascomata 90-150 μ , asci 40-70 x 30-40 μ , spores 20-28 x 10-12 μ , paraphyses (?). Syll. Fung. 24:429.

20. *Seynesia chilensis* Speg., Fungi Chilensis no. 166, p. 107. 1910. *Seynesiola chilensis* Speg., Bol. Acad. Nac. Ci. Cordoba 23:498. 1919. On *Eugenia*, Myrtaceae. Ascomata 250-400 μ , spores 25-28 x 12-14 μ . Öst. Bot. Zeitschr. 63:127. 1913. Syll. Fung. 22:523. 1913.

21. *Seynesia olivascens* Speg., Fungi Puigg. no. 361, Bol. Acad. Nac. Ci. Cordoba 11:569. 1889. On *Drymis*, Magnoliaceae; Myrtaceae; *Xanthoxylum*, Rutaceae. Ascomata 80-90 μ , asci 30 x 12 μ , spores 10-11 x 4 μ , paraphysate. Syll. Fung. 9:1067. 1891.

22. *Seynesia platensis* Speg., Fungi Arg. novi v. crit. p. 298. 1899. On *Duvaua*, Anacardiaceae. Ascomata 300-450 μ , asci 20-25 x 18-20 μ , spores

10-12 x 4-5 μ , aparaphysate. Syll. Fung. 16:639; Öst. Bot. Zeitschr. 63:128. 1913.

23. *Seynesia variolosa* Speg., Fungi Puigg. no. 363, Bol. Acad. Nac. Ci. Cordoba 11:570. 1889. On Myrtaceae. Ascomata 120-150 μ , asci 28-30 x 18-20 μ , spores 12 x 5-6 μ , aparaphysate. Syll. Fung. 9:1067.

24. *Seynesia pulchella* Bomm., Rouss., and Sacc., Syll. Fung. 9:1066. 1891. *Seynesia caronae* Pass., Diag. Fung. nuov., Rend. R. Acad. Lincei, Roma 4, ser. 3, no. 44. 1887. *Arnaudiella caronae* Petr., Ann. Myc. 25:339. 1927. On Sarothamus, Leguminosae; Spartina, Gramineae. Ascomata 45-110 μ , asci 30-36 x 9-13 μ , spores 11-15 x 4-6 μ , aparaphysate.

25. *Seynesia iochromatis* (Rehm) Theiss., Öst. Bot. Zeitschr. 62:279. 1912. *Microthyrium iochromatis* Rehm, Hedw. 35:162. 1895. On Jochroma, Solanaceae. Ascomata 150-230 μ , asci 42-50 x 15-22 μ , spores 16 x 8 μ , aparaphysate. Syll. Fung. 14:688.

26. *Seynesia rimosa* Pat., Bull. Soc. Myc. Fr. 42:230, 1895. On leaves. Ascomata 500-1000 μ , asci 80-90 x 16-20 μ , spores 16-20 x 6 μ , aparaphysate. Syll. Fung. 14:689; Öst. Bot. Zeitschr. 63:127. 1913.

27. *Seynesia disciformis* Pat., Bull. Soc. Myc. Fr. 42:230. 1895. On leaves. Ascomata 300 μ , asci 100 x 20 μ , spores 20 x 7 μ , aparaphysate. Syll. Fung. 14:689; Öst. Bot. Zeitschr. 63:126. 1913.

28. *Seynesia juniperi* (Desm.) Stev., n. comb. Syn. d'apres Winter, Pilze II, Abt. 1. 1887. Ascomycetes, p. 340 in Rabenhorst, Krypt. fl. *Seynesiella juniperi* Arn., Ann. École Nac. Agr. Montp. 16:203. 1918. *Dothidea juniperi* Desm., Ann. Sci. Nat. ser. 2, 15:129. 1841. *Gibbera juniperi* Auersw., Rabh. Fungi Europei, no. 1030. *Stigmathea juniperi* (Desm.) Winter l. c., *Microthyrium juniperi* Sacc., Mich. 1:342. 1877. Syll. Fung. 2:664. *Asterina juniperi* Jacz. and Boyer, Materiaux fl. myc. Montp. 1894. *Stigmathea alpina* Speg., in Thümen, Mycotheca universalis, no. 1057. On Juniperus, Pinaceae. Ascomata 200 μ , asci 65 x 20 μ , spores 20-25 x 7-9 μ , aparaphysate.

29. *Seynesia atkinsonii* Stev. and Ryan, Bernice P. Bishop Mus. Bul. 19:69. 1925. *Myiocopron freycinetiae* (Atk.) Arn., Ann. Crypt. Exot. 4:88. 1931. On Freycinetia, Pandanaceae. Ascomata 120 μ , asci 24-29 x 60-94 μ , spores 12 x 22 μ , aparaphysate.

30. *Seynesia scutellum* Syd., Ann. Myc. 8:40. 1910. On Drymis piperita, Magnoliaceae. Ascomata 350-550 μ , asci 50-70 x 14-20 μ , spores 22-28 x 7-8 μ , aparaphysate. Syll. Fung. 22:524.

31. *Seynesia megalothecia* Speg., Fungi Puigg. no. 360, Bol. Acad. Nac. Ci. Cordoba 11:569. 1889. *Seynesia hammariana* P. Henn., Hedw. 41:301. 1902. On Sebastiania, Euphorbiaceae; Coccoloba, Polygonaceae. Ascomata 1000-2000 μ , asci 40-60 x 40-50 μ , spores 20-30 x 16-20 μ , aparaphysate. Öst. Bot. Zeitschr. 63:126. 1913. Syll. Fung. 9:1067; 17:867.

32. *Seynesia circinans* (Speg.) Theiss., Öst. Bot. Zeitschr. 62:220. 1912; 63:127. 1913. *Microthyrium* (?) *circinans* Speg., Fungi Arg. 4, no. 141, Anal. Soc. Ci. Argentina 12:553. 1881. *Microthyriolum circinans* (Speg.) Speg., Fungi Arg. 4, no. 123; Bol. Acad. Nac. Ci. Cordoba 23:499. 1919. On leaves. Ascomata 200-270 μ , spores 30-32 x 11-14 μ , paraphysate. Hedw. 37:322, fig. 4. 1898. Syll. Fung. 2:665.

33. *Seynesia pachysperma* Speg., Fungi Puigg. no. 362, Bol. Acad. Nac. Ci. Cordoba 11:570. 1889. On leaves. Ascomata 150-200 μ , asci 55-65 x 40-60 μ , spores 32-42 x 18-20 μ , paraphysate. Öst. Bot. Zeitschr. 63:127. 1913. Syll. Fung. 9:1067.

34. *Seynesia santanderiana* Toro, Ann. Myc. 32:111. 1934. On *Rapanea*. Ascomata 200-456 x 171-456 μ , asci 88-136 x 34-46 μ , spores 41-45 x 18-19 μ .

35. *Seynesia plana* (Rac.) Theiss., Abh. K. K. Zool.-Bot. Ges. Wien 7:33. 1913. *Asterina plana* Rac., in herb. No measurements recorded.

36. *Seynesia piraguensis* Speg., Fungi Guar., Pug. I, no. 298. Anal. Soc. Ci. Argentina 17. 1884. On Laurinaceae. Ascomata 170-250 μ , asci globose 45 μ , paraphysate, spores 20-22 x 9-10 μ . Öst. Bot. Zeitschr. 63:127. 1913. Syll. Fung. 9:1064. 1891.

9. SEYNESIOPELTIS Stevens and Ryan

Bernice P. Bishop Museum Bulletin 19:69. 1925.

Type: *S. tetraplasandrae* Stev. and Ryan.

Characters: No free mycelium, ascomata round, radiate, 2-5 mm., thallus setose. Spores 2-celled, brown, ascomata bearing several locules, paraphysate.

Literature: Bernice P. Bishop Mus. Bul. 19:69. 1925. Ann. Crypt. Exot. 4:80. 1931.

1. *Seynesiopeltis tetraplasandra* Stev. and Ryan, *l. c.* On *Tetraplasandra*, Araliaceae. Ascomata 113-227 μ , asci 169-180 x 36-45 μ , spores 21-43 x 12-18 μ .

10. SCUTELLUM Spegazzini

Fungi Puigg., Bol. Acad. Nac. Ci. Cordoba 11:574. 1889.

Type: *S. paradoxum* Speg.

Characters: No free mycelium, ascomata superficial, dimidiate, smooth, ostiolate, paraphysate. Spores brown, 3-4 celled.

Sydow says that this genus is "not certainly" of the Microthyriaceae. In the general description of the genus the character "paraphysate" is given. In the five species listed three are paraphysate and two have paraphyses. Ann. Myc. 15:416. 1917.

Figures: Saccardo, Gen. Pyren. tab. 13, fig. 2. Oudemans, Champ. Pays Bas, tab. 13, fig. 2. Rev. Pyren. Batav. tab. 13, fig. 2.

1. *Scutellum javanicum* v. Höhn., Sitz. K. Acad. Wiss. Wien 121:348. 1912. On Orchidaceae. Ascomata 250-350 μ , asci 64-70 x 33-34 μ , spores 30 x 12 μ , aparaphysate. Syll. Fung. 24:431.

2. *Scutellum paradoxum* Speg., Fungi Arg., Pug. IV. Anal. Soc. Ci. Argentina 11:574. 1889. On leaves. Ascomata 150-180 μ , asci 65-80 x 15 μ , spores 20 x 6.5-7 μ , aparaphysate. Rev. Myc. 4, tab. 28, fig. 10. 1882. Syll. Fung. 2:668. 1886.

3. *Scutellum guaraniticum* Speg., Fungi Guar., Pug. I, no. 301. 1883. On *Pilocarpus*, Rutaceae. Ascomata 130-160 μ , asci 50 x 15-18 μ , spores 12-14 x 5-6 μ , aparaphysate. Spores of *S. javanicum*, 3-septate, those of *S. paradoxum* and *S. guaraniticum*, 2-septate. Bol. Acad. Nac. Ci. Cordoba 23:505. 1919. Syll. Fung. 9:1068. 1891.

4. *Scutellum microsporum* Speg., Ann. Mus. Nac. Buenos Aires 12:427, fig. 30. 1909. On Moya, Celastraceae. Ascomata 200-250 μ , asci 50 x 10 μ , spores 12 x 3-4 μ , 2-septate, paraphysate. Syll. Fung. 22:530.

5. *Scutellum bromeliacearum* (Rehm) Sacc., and Syd., Syll. Fung. 16:645. 1902. *Micropelisis maculata* Cooke and Massee var. *bromeliacearum* Rehm, Hedw. 39:230. 1900. On Bromelia, Bromeliaceae. Ascomata 150 μ , asci 45-50 x 8-10 μ , spores 10-12 x 3-3.5 μ .

11. HALBANIA (Rac.) v. Höhnel

Sitz. K. Akad. Wiss. Wien 118:1168. 1909.

Type: *H. Cyathearum* (Rac.) v. Höhn.

Characters: Ascomata superficial, dimidiate, radiate, ostiolate, aparaphysate, brown basal membrane. Spores brown with two large middle cells and two smaller apical cells.

Literature: Myc. Centralbl. 3:277. 1913. Ann. École Nac. Agr. Montp. 16:164. 1918.

1. *Halbania cyathearum* (Rac.) v. Höhn., l. c. *Asterina cyathearum* Rac., Parasit. Algen und Pilze Javas 2:17. 1900. On Cyathea, Pteridophyta. Ascomata 300 μ , asci 58 x 50 μ , spores 26 x 14 μ . Syll. Fung. 16:649; 17:881.

12. CAENOTHYRIUM Theiss. and Syd.

Annales Mycologici 15:417. 1917.

Type: *C. alang-alang* (Rac.) Theiss. and Syd.

Characters: No free mycelium, ascomata dimidiate, ostiolate, setose, no basal mebrane, aparaphysate. Spores hyaline, many-celled.

Literature: Ann. Myc. 12:561. 1914; 15:417. 1917. Parasit. Algen und Pilze Javas 2:8. 1900.

1. *Caenothyrium alang-alang* (Rac.) Theiss. and Syd., *l. c.* *Micropeltis alang-alang* Rac., Parasit. Algen und Pilze Javas 2:8. 1900. *Microthyrium imperatae* Syd., Ann. Myc. 12:561. 1914. v. Höhnelt regarded it as *Actinopeltis*. On Imperata, Gramineae. Ascomata 100-150 μ , asci 40-50 x 10 μ , spores 12-15 x 2.5 μ .

13. ACTINOMYXA Sydow

Annales Mycologici 15:146. 1917.

Type: *A. australiensis* Syd.

Characters: Ascomata superficial, radiate, no free mycelium, asci 8-spored, paraphysate, spores hyaline, several (3) septate.

1. *Actinomyxa australiensis* Syd., *l. c.* On Lasiopetalum, Sterculiaceae. Ascomata 300-350 μ , asci 56-65 x 8-10 μ , spores 18-22 x 2-4 μ . Syll. Fung. 24:533.

14. PHRAGMOTHYRIUM v. Höhnelt

Sitz. K. Akad. Wiss. Wien 121:347. 1912.

Type: *P. hymenophylli* (Pat.) v. Höhn.

Characters: Like *Microthyrium*, but the spores colorless, many-celled. This genus was segregated by v. Höhnelt from *Micropeltis*, which is of the Hemisphaeriaceae. Study of types is necessary. It is probable that some of the species listed here belong to the Microthyriaceae and some to the Hemisphaeriaceae.

1. *Phragmothyrium trichomanis* (Henn.) v. Höhn., *l. c.* *Micropeltis trichomanis* Henn., Engl. Bot. Jahrb. 28:326. 1900. On Trichomanis, Pteridophyta. Ascomata 200 μ , asci 30-45 x 5-7 μ , paraphysate, spores 1-3 septate. Syll. Fung. 16:645.

2. *Phragmothyrium biseptata* (v. Höhn.) v. Höhn., Sitz. K. Akad. Wiss. Wien 121:347. 1912. *Micropeltis biseptata* v. Höhn., Sitz. K. Akad. Wiss. Wien 118:1168. 1909. On Paratropia, Araliaceae. Ascomata 120-140 μ , asci 30-32 x 6-9 μ , spores 7.5-10 x 2-3 μ , paraphysate. Spores 2-septate. Syll. Fung. 22:527.

The position of this and the preceding species in this genus is questionable due to the few septa in the spores.

3. *Phragmothyrium manaosensis* (P. Henn.) v. Höhn., Sitz. K. Akad. Wiss. Wien 121:347. 1912. *Micropeltis manaosensis* P. Henn., Fungi Amaz. 3:377. 1904. On Myrtaceae. Ascomata 130-160 μ , asci 30-40 x 11-15 μ , spores 10-13 x 3-3.5 μ , spores 2-3 septate. Syll. Fung. 17:869.

4. *Phragmothyrium hymenophylli* (Pat.) v. Höhn., Sitz. K. Akad. Wiss. Wien 121:347. 1912. *Micropeltis hymenophylli* Pat., Bull. Soc. Myc. Fr. 24:126, tab. 9, fig. 4. 1887. On *Hymenophyllum*, Pteridophyta. Ascomata 250-300 μ , asci 50-60 x 10 μ , paraphysate, spores 3-septate. Syll. Fung. 9:1071.

5. *Phragmothyrium myrsines* (Rehm) v. Höhn., Sitz. K. Akad. Wiss. Wien 121:347. 1912. *Micropeltis myrsines* Rehm, Hedw. 39:220, fig. 11. 1900. On *Myrsine*, Myrsinaceae. Ascomata 90-120 μ , asci 50 x 15 μ , spores 15 x 6 μ , paraphysate, spores 3-septate. Syll. Fung. 16:643.

6. *Phragmothyrium flageoletii* (Sacc.) v. Höhn., Sitz. K. Akad. Wiss. Wien 121:347. 1912. *Micropeltis flageoletii* Sacc., Grev. 21:67. 1892. On *Hedera*, Araliaceae; *Ilex*, Aquifoliaceae. Ascomata 300 μ , asci 50-60 x 14-16 μ , paraphysate, spores 18-21 x 5-6 μ , 3-septate.

7. *Phragmothyrium fimbriatum* v. Höhn., Ann. Myc. 17:115. 1919. On *Ardisia*, Myrsinaceae. Ascomata 200 μ , asci 60 x 14 μ , paraphysate, spores 16-20 x 4 μ , 3-septate. Syll. Fung. 24:430.

8. *Phragmothyrium corruscans* (Rehm) Theiss., Broteria 12:76. 1914. *Micropeltis corruscans* Rehm, Philipp. Jour. Sci. 8:255. 1913. On *Syn-drella*, Compositae. Ascomata 100 μ , asci 30 x 10 μ , paraphysate, spores 9-12 x 3-3.5 μ , 3-septate.

9. *Phragmothyrium umbilicata* (Mont.) v. Höhn., Sitz. K. Akad. Wiss. Wien 121:347. 1912. *Micropeltis umbilicata* Mont., Bol. Soc. Roy. Bot. Belg. 39:48. 1900. On *Hederae*, Araliaceae; *Carex*, Cyperaceae. Ascomata 500 μ , asci 36-40 x 15 μ , paraphysate, spores 12 x 3.5 μ , 3-septate. Syll. Fung. 16:644.

10. *Phragmothyrium blyttii* (Rostr.) v. Höhn., Sitz. K. Akad. Wiss. Wien 121:347. 1912. *Micropeltis blyttii* Rostr., Bidr. Ascom. Dovre, p. 6. 1891. On *Andromeda*, Ericaceae. Asci 50 x 12-13 μ , spores 32-34 x 2.5-4 μ , 3-septate, paraphyses (?). Syll. Fung. 11:381.

11. *Phragmothyrium caesalpiniae* (Tassi) v. Höhn., Sitz. K. Akad. Wiss. Wien 121:347. 1912. *Micropeltis caesalpiniae* Tassi, Bull. Lab. Ort. Bot., Siena, 2:28, tab. 6, fig. 4. 1899. On *Caesalpinia*, Leguminosae. Ascomata 180-200 μ , asci 50-60 x 24-25 μ , spores 10-12 x 14 μ , 3-septate, paraphyses (?). Syll. Fung. 16:643.

12. *Phragmothyrium carniolica* (Rehm) v. Höhn., Sitz. K. Akad. Wiss. Wien 121:347. 1912. *Micropeltis carniolica* Rehm, Hedw. 31:307. 1892. On *Pyrola*, Pirolaceae. Ascomata 100-250 μ , asci 36-45 x 15 μ , spores 18-22 x 3 μ , 3-septate, paraphyses (?). Syll. Fung. 11:381.

13. *Phragmothyrium erysiphoides* (Rehm) v. Höhn., Sitz. K. Akad. Wiss. Wien 121:347. 1912. *Micropeltis erysiphoides* Rehm, Hedw. 44:1. 1904. On *Malpighiaceae*. Ascomata 200 μ , asci 50-55 x 8-9 μ , spores 15 x 2-2.5 μ , 3-septate, paraphyses (?). Syll. Fung. 17:869.

14. *Phragmothyrium garciniae* (Henn.) v. Höhn., Sitz. K. Akad.

Wiss. Wien 121:347. 1912. *Micropeltis garciniae* P. Henn., Engl. Bot. Jahr. 31:48. 1903. On *Garcinia*, Guttiferaceae. Ascomata 250-300 μ , asci 40-50 x 10-12 μ , paraphysate, spores 15-20 x 3.5-4 μ , 3-4 septate. Syll. Fung. 17:869.

15. *Phragmothyrium xylopie* (Henn.) v. Höhn., Sitz. K. Akad. Wiss. Wien 121:347. 1912. *Micropeltis xylopie* P. Henn., Fungi Amaz., Hedw. 44:66. 1905. On *Xylopie*, Anonaceae. Ascomata 240-300 μ , asci 40-50 x 8-12 μ , spores 14-20 x 3.5-4.5 μ , 3-5 septate. Syll. Fung. 17:869.

16. *Phragmothyrium sprucei* (Cke.) Ryan, n. comb. *Micropeltis sprucei* Cooke, Syll. Fung. 11:382. 1895. *Microthyrium sprucei* Cooke, Grev. 21:76. 1892. On unknown. Ascomata 500 μ , asci elliptical, spores 3-5 septate, 28-32 x 8-9 μ .

17. *Phragmothyrium oleae* (Togn.) v. Höhn., Sitz. K. Akad. Wiss. Wien 121:347. 1912. *Micropeltis oleae* Togn., Hedw. 34:35. 1895. On *Oleae*, Oleaceae. Ascomata 300 μ , asci 45-55 x 12 μ , spores 27-29 x 4-5 μ , 3-5 septate. Syll. Fung. 11:381.

18. *Phragmothyrium coffeicola* (Henn.) v. Höhn., Sitz. K. Akad. Wiss. Wien 121:347. 1912. *Micropeltis coffeicola* Henn., Hedw. 41:63. 1902. On *Coffea*, Rubiaceae. Ascomata 200-500 μ , asci 26-36 x 12-18 μ , spores 18-30 x 3.5-5 μ , 3-6 septate. Syll. Fung. 17:870.

19. *Phragmothyrium distinctum* (Henn.) v. Höhn., Sitz. K. Akad. Wiss. Wien 121:347. 1912. *Micropeltis distincta* Henn., Engl. Bot. Jahrb. 29:257. 1901. On *Tricalysia*, Rubiaceae. Ascomata 180-250 μ , asci 36-65 x 20-28 μ , spores 25-50 x 4-5 μ , 3-9 septate. Syll. Fung. 17:870.

20. *Phragmothyrium rheediae* (Rehm) v. Höhn., Sitz. K. Akad. Wiss. Wien 121:347. 1912. *Micropeltis rheediae* Rehm, Ann. Myc. 9:368. 1911. On *Rheedia*, Guttiferae. Ascomata 150 μ , asci 40 x 12 μ , spores 20 x 3 μ , 5 septate. Syll. Fung. 24:517.

21. *Phragmothyrium schmidtiana* (Rostr.) v. Höhn., Sitz. K. Akad. Wiss. Wien 121:347. 1912. *Micropeltis schmidtiana* Rostr., Botan. Tidsskr. 24:211. 1902. On *Apostasia*, Orchidaceae. Asci 50-52 x 10-12 μ , paraphysate, spores 20-25 x 5 μ , 5-7 septate. Syll. Fung. 17:870.

22. *Phragmothyrium hirtellae* (Henn.) v. Höhn., Sitz. K. Akad. Wiss. Wien 121:347. 1912. *Micropeltis hirtellae* Henn., Hedw. 47:269. 1908. On *Hirtella*, Rosaceae. Ascomata 200-280 μ , asci 35-45 x 13-18 μ , spores 30-35 x 5 μ , 5-7 septate. Syll. Fung. 22:526.

23. *Phragmothyrium alabamensis* (Earle) v. Höhn., Sitz. K. Akad. Wiss. Wien 121:347. 1912. *Micropeltis alabamensis* Earle, Bull. Torr. Bot. Club 24:359. 1898. On *Magnolia*, Magnoliaceae. Ascomata 300-400 μ , asci 50-60 x 16-20 μ , spores 25-30 x 5 μ , 6 septate. Syll. Fung. 16:642.

24. *Phragmothyrium scheffleri* (Henn.) v. Höhn., Sitz. K. Akad. Wiss. Wien 121:347. 1912. *Micropeltis scheffleri* Henn., Engl. Bot. Jahrb. 28:38. 1900. On *Flacourtiaceae*. Ascomata 300-400 μ , asci 80-110 x 22-30

μ , spores 60-90 x 7-9 μ , 10-11 septate, apapophysate. Syll. Fung. 17:869.

25. *Phragmothyrium marattiae* (Henn.) v. Höhn., Sitz. K. Akad. Wiss. Wien 121:347. 1912. *Micropeltis marattiae* Henn., Hedw. 34:13. 1895. On *Marattia*, Pteridophyta. Asci 60-70 x 10-14 μ , spores 27-35 x 3-4 μ , many septate. Syll. Fung. 11:382.

26. *Phragmothyrium rollinae* (Henn.) v. Höhn., Sitz. K. Akad. Wiss. Wien 121:347. 1912. *Micropeltis rollinae* Henn., Hedw. 43:84. 1904. On *Rollinia*, Anonaceae. Ascomata 100 μ , asci 20-30 x 5-7 μ , spores 15-20 x 2-2.5 μ , many septate, paraphysate. Syll. Fung. 17:868.

15. MICROPELTOPSIS Wainio

Acta Soc. Fenn. 49:218. 1921.

Type: *M. cetraricola* Wain.

Characters: Ascomata dimidiate, radiate, spores 3-many septate, hyaline, apapophysate, lichenicole.

1. *Micropeltopsis cetraricola* Wain., l. ♀. On *Cetraria*, a lichen.

16. LEMBOSIDIUM Spegazzini

Bol. Acad. Nac. Ci. Cordoba 26:342. 1922.

Type: *L. portoricense* Speg.

Characters: No free mycelium, ascomata linear, dimidiate. Asci pseudopapophysate. Spores 2-celled, hyaline.

1. *Lembosidium portoricense* Speg., l. c. On *Coccoloba*, Polygonaceae. Ascomata 200-500 x 72-100 μ , asci 25 x 15-20 μ , spores 10 x 2.5 μ . N. Y. Acad. Sci. 8:23. 1926.

17. AULOGRAPHELLA v. Höhnel

Annales Mycologici 15:367 1917

Type: *A. Epilobii* (Lib.) v. Höhn.

Characters: Ascomata linear; spores hyaline, 2-celled, apapophysate. Like *Aulographum* but lacking free mycelium.

1. *Aulographella epilobii* (Lib.) v. Höhn., l. c. *Aulographum epilobii* Lib., Pl. Crypt. Ard. no. 273. 1834. On *Epilobium*, Onagraceae. Asci 15-20 x 6.5-8 μ , paraphyses indistinct, spores 6-8 x 1.8-2 μ . Duby, Hyster. 1861. Syll. Fung. 2:730. 1886.

2. *Aulographella baumeae* Stev. and Ryan, Bernice P. Bishop Mus. Bul. 19:77. 1925. On *Baumea*, Cyperaceae. Ascomata 100-400 μ , asci 10-14 x 25 μ , spores 2-3 x 9 μ .

18. LEMBOSINA Theissen

Annales Mycologici 11:437. 1913. *Ibid.*, 15:417. 1917.

Type: *L. aulographoides* (Bomm., Rouss., and Sacc.) Theiss.

Characters: No free mycelium, ascomata linear, spores dark, 2-celled, paraphysate. Like *Lembosia* but lacking free mycelium.

1. *Lembosina aulographoides* (Bomm., Rouss., and Sacc.) Theiss., Ann. Myc. 11:437. 1913. *Lembosia aulographoides* Bomm., Rouss., and Sacc., Hedw. 31:304. 1892. On *Rhododendron*, Ericaceae. Ascomata 250-330 μ , asci 45 x 28 μ , spores 15-18 x 6 μ . Syll. Fung. 9:1107.

2. *Lembosina copromya* (Bomm., Rouss., and Sacc.) Theiss., Ann. Myc. 11:437. 1913. *Lembosia copromya* Bomm., Rouss., and Sacc., Syll. Fung. 9:1107. 1891. On *Tilia*, Tiliaceae. Ascomata 400-500 x 200-250 μ , asci 36-60 x 21-27 μ , spores 20-22 x 9-10 μ . Probably a variety of *L. aulographoides*.

19. MORENOINA Theissen

Annales Mycologici 11:434. 1913.

Type: *M. antarctica* (Speg.) Theiss.

Characters: No free mycelium, ascomata linear, spores brown, 2-celled, paraphysate. Like *Morenoella* but lacking free mycelium.

1. *Morenoina microscopica* (Speg.) Theiss., Ann. Myc. 11:434. 1913. *Morenoella microscopica* Speg., Fungi Puigg. no. 373. Bol. Acad. Nac. Ci. Cordoba 11:577. 1889. On *Eugenia*, Myrtaceae. Ascomata 250-1500 μ , asci 15-16 x 7-8 μ , spores 6-7 x 2 μ . Syll. Fung. 9:1096.

2. *Morenoina australis* (Speg.) Theiss., Ann. Myc. 11:434. 1913. *Morenoella australis* Speg., Fungi Puigg. no. 283. Bol. Acad. Nac. Ci. Cordoba 11:240. 1889. On *Poa*, Gramineae. Ascomata 100-150 μ , asci 14-16 x 10-12 μ , spores 6-8 x 2.5-3 μ . Syll. Fung. 9:1096.

3. *Morenoina antarctica* (Speg.) Theiss., Ann. Myc. 11:435. 1913. *Morenoella antarctica* Speg., Fungi Puigg. no. 283, Bol. Acad. Nac. Ci. Cordoba 11:240. 1889. On *Rostkovia grandiflora*, Juncaceae. Ascomata 500-1500 x 200-300 μ , asci 26-27 x 13-14 μ , spores 10 x 3 μ . Syll. Fung. 9:1096.

4. *Morenoina inaequalis* Maubl. and Arn., Ann. École Nac. Agr. Montp. 16:139, tab. 22. 1918. On Myrtaceae. Ascomata 250 x 80-100 μ , asci 22-28 x 9-12 μ , spores 3.5-4 x 8-10 μ . Syll. Fung. 24:430.

5. *Morenoina graphoides* (Sacc. and Berl.) Theiss., Ann. Myc. 11:435. 1913. *Lembosia graphoides* Sacc. and Berl., Misc. Myc. II, p. 6. On *Olea*, Oleaceae. Ascomata 125-500 μ , asci 40-45 x 12-14 μ , spores 12-14 x 6 μ . Syll. Fung. 9:1104.

6. *Morenoina africana* Doidge, Trans. Roy. Soc. So. Afr. 8:242. 1920.

On *Dryopteris*, Pteridophyta. Ascomata 120-400 x 65-100 μ , asci 23-27 x 10-12 μ , spores 12-14 x 5-6.5 μ .

7. *Morenoina lucens* (Harkn.) Theiss., Ann. Myc. 11:435. 1913. *Lembosia lucens* (Harkn.) Sacc., Syll. Fung. 9:1107. 1891. *Aulographum lucens* Harkn., Bul. Cal. Acad. Sci. p. 28, 1884. On *Garrya*, Cornaceae. Ascomata 500-1000 μ , asci 37 x 28 μ , spores 21 x 10 μ .

8. *Morenoina curatellae* (Starb.) Theiss., Ann. Myc. 11:435. 1913. *Morenoella curatellae* Starb., Bih. K. Svenska Vet. Akad. Handl., Stockholm, Afd. III, no. 1., 25:18. 1899. On *Curatella*, Dilleniaceae. Ascomata 200-300 x 100-150 μ , spores 24-27 x 13-16 μ . Syll. Fung. 16:653.

9. *Morenoina serpens* (Pat.) Theiss., Ann. Myc. 11:435. 1913. *Lembosia serpens* Pat., Ann. Jard. Buitenz. I, suppl. p. 122. 1897. On Pteridophyta. Ascomata 500-600 μ , asci 33-40 x 15-23 μ , spores 28 x 8 μ . Syll. Fung. 14:715.

20. THYROSOMA Sydow

Annales Mycologici 19:307. 1921.

Type: *T. pulchellum* Syd.

Characters: No mycelium, ascomata radiate, with numerous hymenia, no basal membrane, asci 8-spored, paraphysate, spores hyaline, 2-celled.

1. *Thyrosoma pulchellum* Syd., l. c. On *Erythroxylum*, Erythroxylaceae. Asci 40-55 x 15-18 μ , spores 16-18 x 5-6 μ .

21. CAMPOA Spegazzini

Bol. Acad. Nac. Ci. Cordoba 25:90. 1921.

Type: *C. pulcherrima* Speg.

Characters: Asci in a stroma, not in cavities.

1. *Campoa pulcherrima* Speg., l. c. On *Temu divaricata*, Myrtaceae. Ascomata 100-125 μ , asci 70 x 15 μ , spores 12 x 5-6 μ .

22. PYCNOPELTIS Sydow

Annales Mycologici 14:365. 1916.

Type: *P. bakeri* Syd.

Characters: No mycelium, ascomata superficial, asci single, paraphysate, 8-spored, spores brown, many-celled.

In the original description Sydow ascribes this genus to the Trichopeltaceae though a year later in the Synoptische Tafeln (88) it is placed in the Microthyriaceae.

1. *Pycnopeltis bakeri* Syd., l. c. On *Ardisia*, Myrsinaceae. Asci 24-28 x 20-24 μ , spores 15-18 x 4.5-6 μ . Syll. Fung. 24:431.

23. STEPHANOTHECA Sydow

Philipp. Jour. Sci. 9:178. 1914.

Type: *S. micromera* Syd.

Characters: No free mycelium, ascomata superficial, radiate, sterile in center, asci single in a peripheral ring zone, 8-spored, paraphysate. Spores colorless, muriform.

This genus was originally described as of the Hemisphaeriaceae, but in the Synoptischen Tafeln (88) it is given as of the Microthyriaceae.

1. *Stephanotheca micromera* Syd., l. c. On *Taxotrophis*, Moraceae. Ascomata 200-300 μ , asci 20-28 x 14-19 μ , spores 11-16 x 4.5-5.5 μ .

2. *Stephanotheca sydowii* Petr., Ann. Myc. 29:246. 1931. On leaves. Ascomata 150-240 μ , asci 40-48 x 23-30 μ , spores 17-24 x 6-8 μ .

24. PYCNODERMA Sydow

Annales Mycologici 12:563. 1914.

Type: *P. bambusinum* Syd.

Characters: Like *Pycnopeltis* except spores hyaline, muriform.

This genus was originally ascribed to the Trichopeltaceae but later appears in the Microthyriaceae in the Synoptischen Tafeln (88).

1. *Pycnoderma bambusinum* H. and P. Syd., l. c. On *Bambusa* and *Schizostachyum*, Gramineae. Asci 24-27 x 20-25 μ , spores 16-18 x 7-9 μ . Syll. Fung. 24:433.

2. *Pycnoderma circinans* Syd., Ann. Myc. 15:236. 1917. On *Bambusa*, Gramineae. Ascomata 150-200 μ , asci 20-28 x 18-22 μ , spores 12-15 x 4.5-6 μ . Syll. Fung. 24:434.

3. *Pycnoderma villaresiae* Syd., Ann. Myc. 15:147. 1917. On *Villaresia*, Icacinaceae. Ascomata 150-220 μ , asci 22-28 x 18-22 μ , spores 13-16 x 3.5-4.5 μ . Syll. Fung. 24:434.

25. CALOTHYRIELLA v. Höhnelt

Ber. Deutsch. Bot. Ges., 35:251. 1917.

Type: *C. pinophylla* v. Höhn.

Characters: Like *Calothyrium* but the spores hyaline, 1-celled, paraphysate.

Literature: Ann. Myc. 15:371. 1917.

1. *Calothyriella osmanthi* Stev. and Ryan, Bernice P. Bishop Mus. Bul. 19:70. 1925. On *Osmanthus*, Oleaceae. Ascomata 90 μ , asci 18 x 10 μ , spores 3-9 x 1-2 μ .

2. *Calothyriella pinophylla* v. Höhn., Ann. Myc. 15:372. 1917. On Pinus, Pinaceae. Ascomata 80-130 μ , asci 36-44 x 7-8 μ , spores 10-13 x 2-2.8 μ . Syll. Fung. 24:436.

26. STEGOTHYRIUM v. Höhnelt

Sitz. K. Akad. Wiss. Wien, I Abt. 127:382. 1918.

Type: *S. denudans* (Rehm) v. Höhn.

Characters: Free mycelium present, ascomata circular, spores 1-celled, hyaline, paraphysate.

1. *Stegothyrium denudans* (Rehm) v. Höhn., l. c. *Myiocopron denudans* Rehm, Hedw. 42:292. 1903. On dead leaves. Ascomata 100-120 μ , asci 35-40 x 7-8 μ , paraphysate, spores 12-15 x 2.5 μ .

27. CALOTHYRIOPELTIS Stevens and Ryan

Bernice P. Bishop Mus. Bul. 19:71. 1925.

Type: *C. scaevolae* Stev. and Ryan.

Synonym: *Calothyris* Clements and Shear (not Stev. and Ryan).

Characters: Free mycelium present, hyphopodiate, spores brown, 1-celled.

1. *Calothyriopeltis clermontiae* Stev. and Ryan, l. c., 1925. On Clermontia, Campanulaceae. Ascomata 90-170 μ , asci 21-29 x 13-38 μ , spores 9 x 18-21 μ .

2. *Calothyriopeltis metrosideri* Stev. and Ryan, l. c., 1925. On Metrosideros, Myrtaceae. Ascomata 270 μ , asci 23-30 x 32-38 μ , spores 9 x 14 μ .

3. *Calothyriopeltis scaevolae* Stev. and Ryan, l. c., 1925. On Scaevola, Goodeniaceae. Ascomata 90-331 μ , asci 25-27 μ , spores 7-9 x 12-16 μ .

28. CAUDELLA Sydow

Annales Mycologici 14:90. 1916.

Type: *C. oligotricha* Syd.

Characters: Hyphopodiate, dimidiate, obscurely radiate, ostiolate, paraphysate, hymenium simple, spores 2-celled, hyaline, caudate.

1. *Caudella oligotricha* Syd., l. c., 1916. On Flacourtiaceae. Ascomata 300-380 μ , asci 85-105 x 16-18 μ , spores 25-34 x 6-7 μ .

2. *Caudella psidii* Ryan, Mycologia 16:179. 1924. On Psidium and Eugenia, Myrtaceae. Ascomata 280-391 μ , asci 96-210 x 19-24 μ , spores 12-14 x 36-48 μ . Ann. Myc. 28:380. 1930.

29. MYCOLANGLOISIA Arnaud

Ann. École Nat. Agr. Montp. 16:157. 1918.

Type: *M. echinata* Arn.

Characters: Like *Trichothyrium*, but bearing erect bristles in the region of the ostiole, and mycelium formed of interwoven filaments instead of ribbon-like thallus.

1. *Mycolangloisia echinata* Arn., *l. c.*, 1918. On a fungus (*Parodiopsis*?). Ascomata 150-170 μ , ostiolate, spores 2-celled, hyaline, 5 x 25 μ , bristles 8-12 in number, 40 μ long.

30. CALOTHYRIUM Theissen

Annales Mycologici 10:160. 1912.

Type: *C. nebulosum* (Speg.) Theiss.

Characters: Mycelium present, non-hyphopodiate, ascomata round, radiate, ostiolate, hymenium simple, paraphysate or aparaphysate, spores 2-celled hyaline.

Literature: Ann. Myc. 25:326. 1927.

Arnaud (Les Asterinees, p. 149) united *Calothyrium* with *Microthyrium*; Sydow (Ann. Myc. 28:150. 1930) does not agree.

Synonymous genera:

1) *Calothyriolum* Speg., Bol. Acad. Nac. Ci. Cordoba 23:499. 1919. *C. caaguazuense* Speg., Fungi Guar. I, no. 296. We see no distinction warranting separating Spegazzini's genus from *Calothyrium*. Some assume that it is the presence or absence of paraphyses, but *C. jaffulianum* Speg. is paraphysate, while *C. aphiphynum* Speg. is aparaphysate.

2) *Leptopeltina* Speg., Bol. Acad. Nac. Ci. Cordoba 27:397. 1923. *L. antarctica* Speg. This genus is not to be distinguished from *Calothyrium*.

Nos. 1-8 paraphysate.

Nos. 9-15 aparaphysate.

Nos. 16-25 paraphyses not recorded.

1. *Calothyrium dryadis* (Rehm) v. Höhn., Ber. Deutsch. Bot. Ges. 37:111. 1919. *Microthyrium microscopicum* Desm. var. *dryadis* Rehm, Ann. Myc. 2:520. 1904. On *Dryas*, Rosaceae. Ascomata 70-90 μ , asci 25 x 7-8 μ , spores 8 x 2-2.5 μ , paraphysate.

2. *Calothyrium leptosporum* Theiss., Broteria 12:21. 1914. On *Solanum*, Solanaceae. Ascomata 100-130 μ , asci 55 x 14 μ , spores 10-12 x 3.5-4 μ , paraphysate. Syll. Fung. 24:39.

3. *Calothyrium aphanellum* Syd., Ann. Myc. 29:222. 1931. On *Leea*, Vitaceae. Ascomata 40-100 μ , asci 18-23 x 12-15 μ , spores 10-13 x 3.5-4 μ , paraphysate.

4. *Calothyrium jaffuelianum* (Speg.) Stev., n. comb. *Calothyriolum jaffuelianum* Speg., Bol. Acad. Nac. Ci. Cordoba 25:89. 1921. On Trevoa, Rhamnaceae. Ascomata 150-250 μ , asci 60-70 x 14-18 μ , spores 12-14 x 6-8 μ , paraphysate.

5. *Calothyrium nebulosum* (Speg.) Theiss., Öst. Bot. Zeitschr. 62:435. 1912. *Seynesia* (?) *nebulosa* Speg., Fungi. Guar. 3:117. 1891. Syll. Fung. 11:381. *Asterinella nebulosa* Theiss., Öst. Bot. Zeitschr. 62:435. 1912. *Calothyrium nebulosum* Arn., Ann. École Nat. Agr. Montp. 16:154. 1918. On Myrsine, Myrsinaceae. Ascomata 200-250 or 220 x 300 μ , asci 50-60 x 10-12 μ , spores 16 x 5-6 μ , paraphysate. Broteria 12:82. 1914; Ann. Myc. 10:177. 1912.

6. *Calothyrium jahnii* Syd., Ann. Myc. 28:147. 1930. On Clidemia, Melastomataceae. Ascomata 150-250 x 70-100 μ , or 80-140 μ , asci 17-28 x 14-16 μ , spores 10-16 μ , paraphysate.

7. *Calothyrium psychotriae* Doidge, Bothalia 1:76. 1921. On Psychotria, Rubiaceae. Ascomata 400-430 μ , asci 50-53 or 60-64 x 30 μ , spores 26-29 x 11.5-13 μ , paraphysate.

8. *Calothyrium subcolliculosum* Speg., Bol. Acad. Nac. Ci. Cordoba 23:502. 1919. On leaves. Ascomata 150-250 μ , asci 80-100 x 30-40 μ , spores 30-32 x 15-16 μ , paraphysate. Syll. Fung. 24:440.

9. *Calothyrium stomatophorum* (Ell. and Mart.) Theiss., Ann. Myc. 10:191. 1912. *Asterella stomatophorum* Sacc., Syll. Fung. 15:55. *Asterina stomatophora* Ell. and Mart., Jour. Myc. 1:98. 1885. On Quercus, Fagaceae. Ascomata 170-185 μ , asci 30-35 x 6-8 μ , spores 7-12 x 2.5-3 μ , paraphysate. Syll. Fung. 9:394.

10. *Calothyrium ingae* Ryan, Mycologia 16:179. 1924. *Microthyrium ingae* (Ryan) Toro, Jour. Dept. Agr. Puerto Rico 10:13. 1926. On Inga, Leguminosae. Ascomata 108 μ , asci 14-17 μ in diameter, spores 2 x 12 μ , paraphysate.

11. *Calothyrium versicolor* (Desm.) Theiss., Öst. Bot. Zeitschr. 62:217. 1912. *Microthyrium versicolor* (Desm.) v. Höhn., Frag. zur. Myk., 518. *Sacidium versicolor* Desm., Ann. Sci. Nat. 20:217. 1853. *Microthyrium rubi* Niessl, Fungi Chilensis 104. 1910. On Rubus, Rosaceae. Ascomata 100 μ , asci 48-50 x 7-8 μ , spores 14 x 4 μ , paraphysate. Syll. Fung. 2:663. 1886.

12. *Calothyrium apiahynum* (Speg.) Stev., n. comb. *Calothyriolum apiahynum* Speg., Bol. Acad. Nac. Ci. Cordoba 23:503. 1919. On Persea (?), Lauraceae. Ascomata 90-100 μ , asci 40 x 35 μ , spores 20 x 9 μ , paraphysate. Syll. Fung. 24:441.

13. *Calothyrium vile* Syd., Philipp. Jour. Sci. 21:142. 1922. On Phoebe, Lauraceae. Ascomata 150-300 μ , asci 50-80 x 18-22 μ , spores 18-24 x 9-12 μ , paraphysate.

14. *Calothyrium suttoniae* Stev. and Ryan, Bernice P. Bishop Mus.

Bul. 19:71. 1925. On *Suttonia*, Myrsinaceae. Ascomata 79-217 μ , asci 39-45 x 27-30 μ , spores 9 x 27 μ , paraphysate.

15. *Calothyrium jodascum* Speg., Bol. Acad. Nac. Ci. Cordoba 23:501. 1919. On *Aniba*, Lauraceae. Ascomata 100-150 μ , spores 20-30 x 15-16 μ . Syll. Fung. 24:439.

16. *Calothyrium ryani* Stev., n. name. *Calothyrium psychotriae* Ryan, Mycol. 16:179. 1924. (Not *C. psychotriae* Doidge). *Microthyrium psychotriae* Toro, Jour. Dept. Agr. Puerto Rico 10:13. 1926. On *Psychotria*, Rubiaceae. Ascomata 112 μ , asci 12 μ , spores 2 x 5 μ .

17. *Calothyrium pinastri* (Fckl.) Theiss., Öst. Bot. Zeitschr. 62:219. 1912. *Microthyrium pinastri* Fckl., Symb. Myc., App. 3, 29:876. Syll. Fung. 2:664. 1886. *Micropeltis pinastri* (Fckl. and Karst.) v. Höhn., Frag. no. 518. On *Pinus*, Pinaceae. Ascomata 140-250 μ , asci 16-20 x 4 μ , spores 8 x 1.3-1.6 μ . Conidia: Sirothyriella.

18. *Calothyrium osmanthi* Stev. and Ryan, Bernice P. Bishop Mus. Bul. 19:71. 1925. On *Osmanthus*, Oleaceae. Ascomata 75-180 μ , spores 1-3 x 7-9 μ .

19. *Calothyrium antarcticum* (Speg.) Stev., n. comb. *Leptopeltina antarctica* Speg., Bol. Acad. Nac. Ci. Cordoba 27:397. 1923. On *Festuca*, Gramineae. Ascomata 75-100 μ , spores 8-9 x 1.5 μ .

20. *Calothyrium hippocrateae* Ryan, Mycologia 16:179. 1924. *Microthyrium hippocratea* Toro, Jour. Dept. Agr. Puerto Rico 10:13. 1926. On *Hippocratea*, Hippocrataceae. Ascomata 84-96 μ , asci 14 x 17-19 μ , spores 2 x 12 μ .

21. *Calothyrium wrightii* (B. and C.) Theiss., Abh. K. K. Zool.-Bot. Ges. 7:117. 1913. *Asterina wrightii* B. and C., Grev. 4:10. 1875. On Cucurbitaceae. Ascomata 170-230 μ , asci 40-55 x 10-18 μ , spores 12-13 x 4.5-5 μ . Syll. Fung. 1:49; Broteria 12:73. 1913.

22. *Calothyrium* (?) *bullatum* (B. and C.) Theiss., Öst. Bot. Zeitschr. 62:217. 1912. *Microthyrium bullatum* v. Höhn., Frag. zur. Myk. 516. *Asterina bullata* B. and C., Jour. Linn. Soc. 10:374. 1869. Syll. Fung. 1:51. *Asterella bullata* B. and C. (sub *Asterina*). Syll. Fung. 1:45. 1882; 14:699. 1899. *Microthyrium albigenum* B. and C., Syll. Fung. 2:666. 1886. On *Peperomia*, Piperaceae. Spores 15 x 2.5 μ .

23. *Calothyrium confertum* (Theiss.) Theiss., Öst. Bot. Zeitschr. 62:276. 1912. *Microthyrium confertum*. Theiss., Ann. Myc. 7:352. 1909. On *Myrrhinium*, Myrtaceae. Ascomata 150-200 μ , asci 42-45 x 16-18 μ , spores 12-15 x 8-11 μ .

24. *Calothyrium pustulata* (E. and M.) Theiss., Ann. Myc. 10:191. 1912. *Asterina pustulata* Ellis, Amer. Nat. 18:1148. 1884. *Asterella pustulata* Sacc., Syll. Fung. 9:395. On *Quercus*, Fagaceae. Ascomata 500-750 μ , asci 55-60 or 27-32 x 10 μ , spores 30-40 x 10-12 μ .

25. *Calothyrium aspersum* (Berk.) Theiss., Öst. Bot. Zeitschr. 62:219. 1912. *Microthyrium aspersum* v. Höhn., Frag. zur. Myk. no. 517. *Asterina aspersa* Berk., Syll. Fung. 1:45. 1882. On *Laurus*, Lauraceae. Spores 12-13 μ long.

31. APHANOPELTIS Sydow

Annales Mycologici 25:82. 1927.

Type: *A. phoebes* Syd.

Characters: Mycelium superficial, non-hyphopodiate, ascomata orbicular, radiate, basal membrane subhyaline, asci 8-spored, mucose-paraphasoid, spores 1-septate, hyaline.

1. *Aphanopeltis phoebes* Syd., l. c. On *Phoebe*, Lauraceae. Ascomata 60-130 μ , asci 20-30 x 12-17 μ , spores 8-12 x 5 μ .

32. PARASTERINA Theiss. and Sydow

Annales Mycologici 15:246. 1917.

Type: *P. melastomatis* (Lév.) Theiss.

Characters: Free mycelium present, hyphopodiate or bearing nodes; hymenium simple; ascomata radiate, not encrusted, round; spores brown, 2-celled; mycelial conidia 1-celled or lacking, paraphyses present, basal membrane present or lacking.

Synonymous genera:

1) *Maublancia* Arn., Ann. École Nat. Agr. Montp. 16:165. 1918. Type: *M. myrtaccarum* Arn. I see no sufficient distinction from *Parasterina*.

2) *Wardinia* Arn., Ann. École Nat. Agr. Montp. 16:165. 1918. It is a *Parasterina* with intercalary hyphopodia. Syll. Fung. 24:476.

1. *Parasterina bredmeyerae* (Rehm) Theiss., Ann. Myc. 15:421. 1917. *Asterina marmellensis* Theiss., Frag. brasil. no. 134. *Seynesia marmellensis* Henn., Hedw. 43:375. 1904. *Asterina bredmeyerae* Rehm, Hedw. 40:161. 1901. On *Bredmeyera*, Polygalaceae; *Sweetia*, Leguminosae. Ascomata 250-300 μ , asci 40-70 x 15-25 μ , spores 14-22 x 7-10 μ . Syll. Fung. 16:1142. 1902; 17:866. 1905; Öst. Bot. Zeitschr. 63:123. 1913; Abh. K. K. Zool.-Bot. Ges. 7:39. 1913.

2. *Parasterina myiocoproides* (Sacc. and Berl.) Theiss., Ann. Myc. 15:421. 1917. *Asterina myiocoproides* Sacc. and Berl., Rev. Myc. 7:1885. *Wardinia myiocoproides* Arn., Ann. École Nat. Agr. Montp. 16:165. 1918. On *Melastomataceae*; *Bromeliaceae*. Ascomata .5 mm., asci 50-60 x 20-22 μ , spores 26-28 x 10-12 μ . Abh. K. K. Zool.-Bot. Ges. 7:39. 1913.

3. *Patasterina pemphidioides* (Cooke) Theiss., Ann. Myc. 15:246.

1917. *Asterina pemphidioides* Cooke, Grev. 5:16. 1876. Syll. Fung. 1:40. *Asterina hobsoni* Berk., in herb. Kew, Hobson no. 6. *Asterina crustosa* B. and Cke., Grev. 21:76. 1892. Syll. Fung. 11:255. *Meliola fumago* Niessl, Hedw. 20:99. 1881. *Dimerosporium fumago* Sacc., Syll. Fung. 1:53. 1882. *Dimerium* S. and S., Syll. Fung. 18:357. 1906; *Lembosia* Wint., Flora 67:266. 1884; *Asterina* v. Höhn., Frag. zur. Myk. no. 54. On *Eugenia*, Myrtaceae; *Celastrus*, Celastraceae. Ascomata 250-400 or 500 x 300-350 μ , asci 60-95 x 50-65 μ , spores 32-40 x 14-16 μ . Abh. K. K. Zool.-Bot. Ges. 7:40. 1913.

4. *Parasterina myrtacearum* (Arn.) Stev., n. comb. *Maublancia myrtacearum* Arn., Ann. École Nat. Agr. Montp. 16:159. 1918. On Myrtaceae. Ascomata 300-450 μ , asci 70-90 x 25-30 μ , spores 30-35 x 14-16 μ . Bull. Soc. Myc. Fr. 36:39. 1920. Syll. Fung. 24:487.

5. *Parasterina ramosii* Syd., Ann. Myc. 15:246. 1917. *Microthyrium ramosii* Syd., Ann. Myc. 15:238. 1917. On *Eugenia*, Myrtaceae. Ascomata 200-300 μ , to 600 x 200-250 μ , asci 50-80 x 35-48 μ , spores 26-30 x 12-14 μ . Syll. Fung. 24:478.

6. *Parasterina jasminicola* (Yates) Mendoza, Philipp. Jour. Sci. 49:449. 1932. *Asterina jasminicola* Yates, Philipp. Jour. Sci. 13:373. 1918. On *Jasminium*, Oleaceae. Asci 22-26 μ , spores 17-19 x 8-10 μ . Syll. Fung. 24:464.

7. *Parasterina lobeliae* (Stev. and Ryan) Stev., n. comb. *Asterina lobeliae* Stev. and Ryan, Bernice P. Bishop Mus. Bul. 19:74. 1925. On *Lobelia*, Campanulaceae. Ascomata 216 μ , asci 9-14 x 39-54 μ , spores 3-5 x 12-14 μ .

8. *Parasterina canthii* (Yates) Mendoza, Philipp. Jour. Sci. 49:446. 1932. *Asterina canthii* Yates, Philipp. Jour. Sci. 13:372. 1918. On *Canthium*, Rubiaceae. Ascomata 90-175 μ , asci 30-40 x 8-10 μ , spores 10-12 x 3-3.5 μ , hyphopodia opposite, 1-celled, oblong-cylindric, 4-5 x 5 μ . Syll. Fung. 24:468.

9. *Parasterina rhabdodendri* (Syd.) Stev., n. comb. *Asterina rhabdodendri* Syd., Ann. Myc. 14:92. 1916. On *Rhabdodendron*, Rutaceae. Ascomata 130-200 μ , asci 35-45 x 32-40 μ , spores 23-26 x 12-15 μ , hyphopodia opposite, cylindric, entire, 1-celled. Syll. Fung. 24:469.

10. *Parasterina transiens* (Theiss.) Theiss., Ann. Myc. 15:421. 1917. *Asterina transiens* Theiss., Abh. K. K. Zool.-Bot. Ges. 7:42, tab. 6, figs. 29-30 and tab. 8, fig. 6, 1913. On *Miconia*, Melastomataceae. Ascomata 150-220 μ , or 250-340 x 170-220 μ , asci 32-40 x 22 μ , spores 17-19 x 6-8 μ , hyphopodia alternate, 1-celled, straight, rod-shaped.

11. *Parasterina eugeniae* (Yates) Mendoza, Philipp. Jour. Sci. 49:448. 1932. *Asterina eugeniae* Yates (not *A. eugenia* Mont. or Thüm.), Philipp. Jour. Sci. 12:371. 1917. On *Eugenia*, Myrtaceae. Ascomata 225-275 μ ,

asci 50-60 x 20-22 μ , spores 20 x 5 μ , hyphopodia alternate, cylindric, 10-12 x 6 μ . Syll. Fung. 24:461.

12. *Parasterina fagarae* (Yates) Mendoza, Philipp. Jour. Sci. 49:448. 1932. *Asterina fagarae* Yates, Philipp. Jour. Sci. 13:373. 1918. On *Fagara*, Rutaceae. Ascomata 170-220 μ , asci 50-55 x 35-40 μ , spores 22-25 x 11-13 μ , hyphopodia alternate, cylindric, 10-15 x 4-5 μ . Syll. Fung. 24:469.

13. *Parasterina tayabensis* (Yates) Mendoza, Philipp. Jour. Sci. 49:454. 1932. *Asterina tayabensis* Yates, Philipp. Jour. Sci. 12:372. 1917. On leaves. Ascomata 130-200 μ , asci 25-30 μ , spores 22-10 μ , hyphopodia cylindric, alternate 10-12 x 5-7 μ . Syll. Fung. 24:475.

14. *Parasterina nycticali* (Yates) Mendoza, Philipp. Jour. Sci. 49:450. 1932. *Asterina nycticali* Yates, Philipp. Jour. Sci. 12:371. 1917. On *Nycticalos*, Bignoniaceae. Ascomata 90-110 μ , asci 26-28 x 18-20 μ , spores 15-18 x 7-8 μ , hyphopodia alternate, 1-celled, lobed, 10-11 x 12-15 μ . Syll. Fung. 24:445.

15. *Parasterina momordicae* (Yates) Mendoza, Philipp. Jour. Sci. 49:450. 1932. *Asterina momordicae* Yates, Philipp. Jour. Sci. 13:374. 1918. On *Momordica*, Cucurbitaceae. Ascomata 80-90 μ , asci 35-40 x 22-24 μ , spores 19-21 x 9-11 μ , hyphopodia 1-celled, alternate, lobed, 8-12 μ . Syll. Fung. 24:449.

16. *Parasterina japonica* (Theiss.) Theiss., Ann. Myc. 15:421. 1917. *Asterina japonica* Theiss., Abh. K. K. Zool.-Bot. Ges. 7:43, tab. 6, figs. 22-23 and tab. 8, fig. 8, 13, 14. 1913. On *Elaeagnus*, Elaeagnaceae. Ascomata 140-200 μ , asci 45-68 x 25-30 μ , spores 20-23 x 9-11 μ , hyphopodia 1-celled, lobed, alternate. Syll. Fung. 24:451.

17. *Parasterina sydowii* (Syd.) Stev., n. comb. *Asterina melanotes* Syd., Ann. Myc. 27:59. 1929; not *P. melanotes* Syd., Philipp. Jour. Sci. 21:142. 1922. On *Blakea*, Melastomataceae. Ascomata 180-300 μ , asci 48-65 x 30-45 μ , spores 17-28 x 10-14.5 μ , hyphopodia 1-celled, lobed, alternate.

18. *Parasterina astroniae* (Yates) Mendoza, Philipp. Jour. Sci. 49:446. 1932. *Asterina astroniae* Yates, Philipp. Jour. Sci. 12:370. 1917. On *Astronia*, Melastomataceae. Ascomata 160-200 μ , 45-55 x 28-35 μ , spores 18-28 x 10-12 μ , hyphopodia alternate, 1-celled, ovoid or lobed, 5-6 x 4-6 μ . Syll. Fung. 24:458.

19. *Parasterina melastomatis* (Lév.) Theiss., Ann. Myc. 15:246. 1917. *Asterina melastomatis* (Lév.) Ann. Sci. Nat. 3:59. 1845. On *Miconia*, Melastomataceae. Ascomata 250-320 μ , asci 42-50 x 26-30 μ , spores 26-30 x 11-13 μ , hyphopodia 1-celled, lobed, alternate. Syll. Fung. 1:51; Abh. K. K. Zool.-Bot. Ges. 7:43. 1913; Est. Agr. Moca no. 14.

20. *Parasterina cipadessae* (Yates) Mendoza, Philipp. Jour. Sci.

49:446. 1932. *Asterina cipadessae* Yates, Philipp. Jour. Sci. 12:371. 1917. On Cipadessa, Meliaceae. Ascomata 150-250 μ , asci 35-45 x 22-27 μ , spores 28-32 x 10-12 μ , hyphopodia alternate or opposite, lobed, 7-10 μ . Syll. Fung. 24:460; Ann. Myc. 29:225. 1931.

21. *Parasterina hypophylla* (Schw.) Theiss., Ann. Myc. 15:421. 1917. *Asterina hypophylla* (Schw.) Berk., Ann. Myc. 10:165. 1912. *Dothidea hypophylla* Schw., in herb. On Melastomataceae. Ascomata 220-300 μ , asci 58-68 x 36-50 μ , spores 28-32 x 13-16 μ , hyphopodia 1-celled, lobed, cover straight. Abh. K. K. Zool.-Bot. Ges. 7:44. 1913.

22. *Parasterina saccardoana* (Theiss.) Theiss., Ann. Myc. 15:421. 1917. *Asterina saccardoana* Theiss., Abh. K. K. Zool.-Bot. Ges. 7:45. 1913. On Sideroxylon, Sapotaceae. Asci 80-100 x 55-80 μ , spores 46-53 x 22-26 μ , hyphopodia 1-celled, entire, irregular, cover straight. Syll. Fung. 24:471.

23. *Parasterina melastomataceae* (Henn.) Theiss., Ann. Myc. 15:421. 1917. *Asterina melastomataceae* Theiss., Frag. brasil. no. 127. *Scynesia melastomataceae* Henn., Ann. Myc. 10:165. 1912. Syll. Fung. 17:866. *Lembosia melastomatum* Lév., var. *asterinoides* Rehm, in Rick. F. Austro-Amer. 177. *Asterina usterii* Maire, Ann. Myc. 6:146, fig. 3. 1908. On Miconia, Melastomataceae; Euphorbiaceae; Zollnerina, Leguminosae. Asci 38-58 x 20-30 μ , spores 18-22 x 7-10 μ , hyphopodia 1-celled, entire, regular, cover straight. Syll. Fung. 22:542; Abh. K. K. Zool.-Bot. Ges. 7:46. 1913; Öst. Bot. Zeitschr. 63:123. 1913.

24. *Parasterina dilleniaae* (Syd.) Mendoza, Philipp. Jour. Sci. 49:447. 1932. *Asterina dilleniaae* Syd., Philipp. Jour. Sci. 9:181. 1914. On Dillenia, Dilleniaceae. Ascomata 140-200 μ , asci 40-60 x 35-45 μ , spores 20-25 x 10-12 μ , hyphopodia alternate, 1-celled, globose, 10-15 x 9-11 μ . Syll. Fung. 24:449.

25. ***Parasterina miconiae*** (Theiss.) Stev., n. comb. *Asterina miconiae* Theiss., Ann. Myc. 11:440. 1913. On Miconia and Clidemia, Melastomataceae. Ascomata 150-220 μ , asci 50 x 22-28 μ , spores 20-25 x 9-11 μ . Hyphopodia alternate, 1-celled, cylindrical or globose. Syll. Fung. 24:459; Jour. Dept. Agr. Puerto Rico 13-14:231. 1930.

26. *Parasterina platystoma* (Cke. and Mass.) Theiss., Ann. Myc. 15:421. 1917. *Asterina platystoma* Cke. and Mass., Grev. 18:6. 1889. On Castanospermum, Leguminosae. Ascomata 140-170 μ , or 160-280 μ , asci 40-48 x 28-34 μ , spores 22-26 x 8-11 μ , hyphopodia 1-celled, entire, regular, cover mycelium straight. Syll. Fung. 9:382; Abh. K. K. Zool.-Bot. Zeitschr. 7:47. 1913.

27. ***Parasterina holocalycis*** (Speg.) Stev., n. comb. *Asterina holocalycis* Speg., Ann. Mus. Nac. Buenos Aires 23:81. 1912. On Holocalyx, Leguminosae. Ascomata 100-150 μ , asci 50 x 25-30 μ , spores 22-26 x 8-10 μ , hyphopodia alternate, 1-celled, subglobose, 12-15 μ , verrucose. Syll. Fung. 24:457.

28. *Parasterina colliculosa* (Speg.) Theiss., Ann. Myc. 15:421. 1917. *Asterina colliculosa* Speg., Fungi Puigg. no. 347, Bol. Acad. Nac. Ci. Cordoba 11:559. 1889. Syll. Fung. 9:386. 1891. On *Eugenia*, Myrtaceae; *Weinmannia*, Cunoniaceae. Ascomata 200-250 μ , asci 67-70 x 30-40 μ , spores 28-39 x 14-15 μ , hyphopodia 1-celled, entire, regular, cover mycelium straight.

Var. macrospora Stev. n. comb. *Asterina colliculosa* Speg. var. *macrospora* Theiss. *Asterina paraphysata* Wint., Hedw. 31:103. 1892. On leaves. Syll. Fung. 11:256; Abh. K. K. Zool.-Bot. Ges. 7:48. 1913.

29. *Parasterina rigida* Doidge, Trans. Roy. Soc. So. Afr. 8:246. 1921. On *Oncinotis*, Apocynaceae. Ascomata 250-400 μ , asci 60-75 x 30-40 μ , spores 27-33 x 13-15 μ .

30. *Parasterina puttemansii* (Henn.) Theiss., Ann. Myc. 15:421. 1917. *Asterina puttemansii* Theiss., Abh. K. K. Zool.-Bot. Ges. 7:49. 1913. *Asterella puttemansii* Henn., Hedw. 48:11. 1908. *Asterina mandaquiensis* Henn., Hedw. 48:12. 1908. *Seynesia colliculosa* Rehm (not Speg.), Hedw. 37:324. 1898. Syll. Fung. 16:640. On Myrtaceae. Ascomata 250-450 μ or 350-450 x 200-280 μ , asci 52-64 x 35-42 μ , spores 26-32 x 10-13 μ , hyphopodia 1-celled, entire, regular. Syll. Fung. 24:461; Öst. Bot. Zeitschr. 63:121. 1913.

31. *Parasterina consimilis* (v. Höhn.) Theiss., Ann. Myc. 15:421. 1917. *Asterina consimilis* v. Höhn., Sitz. K. Akad. Wiss. Wien, Abt. I, 118:862. 1909. On leaves. Ascomata 200-250 μ , asci 45-50 x 24-25 μ , spores 27-28 x 13 μ , hyphopodia 1-celled, entire, regular. Syll. Fung. 22:543; Abh. K. K. Zool.-Bot. Ges. 7:50. 1913.

32. *Parasterina laxa* Doidge, Bothalia 2:201. 1927. *Parasterina brachystoma* (Rehm) Theiss. var. *laxa* Doidge, Trans. Roy. Soc. So. Afr. 7:245. 1920. On *Grumilea*, *Oxyanthus*, *Plectronia*, Rubiaceae. Ascomata 200-350 μ , asci 53-65 x 40-50 μ , spores 30-33 x 15-16.5 μ , hyphopodia alternate, 1-celled, entire, regular.

33. *Parasterina maublancii* (Arn.) Stev., n. comb. *Asterina maublancii* Maub., Bull. Soc. Myc. Fr. 36:38. 1920. *Asterina melastomatis* Lév. var. *maublancii* Arn., Ann. École Nac. Agr. Montp. 16:169. 1918. On Melastomataceae. Asci 65-82 x 38-48 μ , spores 30-35 x 12-16 μ , hyphopodia 1-celled, ovoid. Syll. Fung. 24:460.

34. *Parasterina implicata* Doidge, Trans. Roy. Soc. So. Afr. 8:244. 1921. On *Sideroxylon*, Sapotaceae. Ascomata 300-400 μ , asci 57-73 x 50-57 μ , spores 35-40 x 13-15 μ , hyphopodia 1-celled, entire, regular.

35. *Parasterina melanotes* Syd., Philipp. Jour. Sci. 21:142. 1922. On *Polyosoma*, Saxifragaceae. Ascomata 400-700 μ , asci 60-85 x 50-60 μ , spores 35-40 x 17-19 μ , hyphopodia 1-celled, regular.

36. *Parasterina brachystoma* (Rehm) Theiss., Ann. Myc. 15:420. 1917. *Asterina brachystoma* Theiss., Öst. Bot. Zeitschr. 63:121. 1913.

Seynesia brachystoma Rehm, Hedw. 37:325. 1898. *Asterina multiplex* Rehm, Asco. no. 1706. *Asterina megalosperma* Speg., Rev. Mus. La Plata 15:27. 1896. Ule 1143, Herh. Pasz., sub *Asterina paraguayensis* Speg. On *Styrax*, *Styraceae*; *Eugenia*, *Myrtaceae*; *Anonaceae*. Ascomata 250 μ , asci 60-70 x 40-50 μ , spores 35-40 x 11-15 μ . Syll. Fung. 22:541.

37. *Parasterina samarensis* (Yates) Mendoza, Philipp. Jour. Sci. 49:453. 1932. *Asterina ramosii* Yates, Philipp. Jour. Sci. 13:373. 1918. On *Dillena*, *Dilleniaceae*. Ascomata 80-120 μ , asci 18-20 x 15-17 μ , spores 14-16 x 6-8 μ .

38. *Parasterina litseae* (Yates) Mendoza, Philipp. Jour. Sci. 49:448. 1932. *Asterina litseae* Yates, Philipp. Jour. Sci. 13:373. 1918. On *Litsea*, *Lauraceae*. Ascomata 100-140 μ , asci 28-30 x 18-24 μ , spores 15-17 x 8-9 μ . Syll. Fung. 24:455.

39. *Parasterina homalomeae* Mendoza, Philipp. Jour. Sci. 49:448. 1932. On *Homalomea*, *Araceae*. Ascomata 180-223 x 120-403 μ , asci 22-26 μ , spores 14-20 x 8-11 μ .

40. *Parasterina spinosa* Mendoza, Philipp. Jour. Sci. 49:453. 1932. On *Cissus*, *Vitaceae*. Ascomata 95-172 μ , asci 35-46 x 29-31 μ , spores 22-25 x 9-10 μ .

41. *Parasterina africana* v. Byl, So. Afr. Jour. Sci. 26:319. 1929. On *Cola*, *Sterculiaceae*. Ascomata 80-210 μ , asci 24-28 μ , spores 18-24 x 8-12 μ .

42. *Parasterina tonduzi* (Speg.) Ryan, n. comb. *Asterina tonduzi* Syd., Ann. Myc. 25:74. 1927. *Opeasterinella tonduzi* Speg., Bol. Acad. Nac. Ci. Cordoba 23:571. 1919. On *Xylosoma*, *Flacourtiaceae*. Ascomata 80-100 μ , asci 40-45 x 40 μ , spores 20-24 x 10-12 μ , paraphysate. Syll. Fung. 24:487.

33. ENGLERULASTER v. Höhnelt

Frag. z. Myk. 10:520. Sitz. K. Akad. Wiss. Wien 119:454. 1910.

Type: *E. orbicularis* (B. and C.) v. Höhn.

Characters: Ascomata astomate, mucose dissolving, paraphysate.

This genus differs from *Asterina* only in that the ascomata undergo a slimy dissolution.

Literature: Broteria 12:78. 1914.

1. *Englerulaster baileyi* (B. and Br.) Theiss., Abh. K. K. Zool.-Bot. Ges. 7:21. 1913. *Asterina baileyi* B. and Br., Proc. Linn. Soc. N. S. Wales 5:89. 1860. *Asterina nigrata* Cooke, in herb. *Asterella hakeae* McAlp., Proc. Linn. Soc. N. S. Wales 22:37. 1897. On *Hakea*, *Proteaceae*. Ascomata 180-240 μ or 180 x 340 μ , asci 65-85 x 28-30 μ , spores 20-24 x 8-9 μ . Syll. Fung. 9:380, 14:699; Broteria 12:80. 1914; Ann. Myc. 10:22. 1912.

2. *Englerulaster orbicularis* (B. and C.) v. Höhn., Sitz. K. Akad. Wiss. Wien 119:454. 1910. *Asterina orbicularis* B. and C., Grev. 4:8. 1875. Rabh.-Wint., Fung. Eur. no. 3439. *Dimerosporium orbiculare* Mart., Jour. Myc. 1:146. 1885. Ell. and Ev., N. Amer. Pyren. Bull. Torr. Bot. Club 18:32. 1891. On *Ilex*, Prinos, Aquifoliaceae. Ascomata 150-170 μ , asci 54-57 x 44-50 μ , paraphysate, spores 33-36 x 15-18 μ . Syll. Fung. 1:46; Trans. Roy. Soc. So. Afr. 8:243. 1920; Broteria 11:78. 1913.

34. ENGLERA Stevens, new genus

Type: *E. atrides* (Syd.) Stev.

Characters: Like *Englerulaster* except for the absence of paraphyses.

1. *Englera atrides* (Syd.) Stev., n. comb. *Englerulaster atrides* Syd., Ann. Myc. 15:239. 1917. On *Modecca*, Passifloraceae. Ascomata 100-150 μ , asci 40-60 x 35-40 μ , spores 24-27 x 11-12 μ . Syll. Fung. 24:490; Ann. Myc. 29:245. 1927.

2. *Englera popowiae* (Doidge) Stev., n. comb. *Englerulaster popowiae* Doidge, Trans. Roy. Soc. So. Afr. 8:243. 1920. On *Popowia*, Anonaceae. Ascomata 160-190 μ , asci 40-47 x 30-40 μ , spores 21-27 x 10-13.5 μ .

3. *Englera continuus* (H. and P. Syd.) Stev., n. comb. *Dimerosporium continuus* Arn., Ann. École Nat. Agr. Montp. 16:178. 1918. *Englerulaster continuus* H. and P. Syd., Ann. Myc. 12:201. 1914. On *Ilex*, Aquifoliaceae. Ascomata 200-300 μ , asci 55-75 x 40-50 μ , spores 25-34 x 12-16 μ . Syll. Fung. 24:490.

4. *Englera gymnosporiae* (Henn.) Stev., n. comb. *Englerulaster gymnosporiae* Theiss., Beiheft. Bot. Centralbl. Abt. II. 29:54. 1913. *Dimerosporium gymnosporium* Sacc., Syll. Fung. 16:408. 1902; Ann. Myc. 7:546. 1909. *Dimerosporium gymnosporiae* Henn., Ann. Nat. Hofmus. Wien p. 3. 1900. On *Gymnosporia*, Celastraceae. Ascomata 90-110 μ , spores 18-24 x 10-13 μ . Broteria 12:80. 1914; Trans. Roy. Soc. So. Afr. 5:719. 1917.

5. *Englera sinensis* (Syd.) Stev., n. comb. *Englerulaster sinensis* Syd., Ann. Myc. 20:62. 1920. On *Ilex*, Aquifoliaceae. Asci 50-60 x 35-50 μ , spores 34-38 x 17-19 μ , paraphysate.

6. *Englera alpinus* (Rac.) Stev., n. comb. *Englerulaster alpinus* Theiss., Abh. K. K. Zool.-Bot. Ges. 7:19. 1913. *Asterina alpina* Rac., Parasit. Algen und Pilze Javas 3:34. 1900. On *Acrondia*, Eleocarpaceae. Ascomata 400 μ , asci 68-80 x 50-52 μ , spores 38 x 17 μ .

7. *Englera asperulispora* (Gaill.) Stev., n. comb. *Englerulaster asperulispora* Gaill., Bull. Soc. Myc. Fr. 13:180. 1897. *Asterella opulenta* Henn., Hedw. 43:83. 1904. *Asterina opulenta* Sacc., Syll. Fung. 17:876. 1905. *Asterina asperulispora* Gaill. Bull. Soc. Myc. Fr. 13:180. 1897. On

Ilex, Aquifoliaceae. Ascomata 120-150 μ , asci 60-80 x 40-60 μ , spores 32-40 x 14-17 μ . Syll. Fung. 14:694; N. Y. Acad. Sci. 8:22. 1926.

8. *Englera orbiculata* (McAlp.) Stev., n. comb. *Englerulaster orbiculatum* McAlp., Beiheft. Bot. Centralbl. 29:53. 1913. *Dimerosporium orbiculatum* McAlp., Linn. Soc. N. S. Wales 28:97. 1903. *Dimerium orbiculatum* Sacc., Syll. Fung. 17:537. 1905. On *Grevillea*, Proteaceae. Ascomata 70-90 μ , asci 50-55 μ , spores 30-35 x 10-12 μ .

9. *Englera ulei* (Wint.) Stev., n. comb. *Englerulaster ulei* Theiss., Beiheft. Bot. Centralbl. 29:51. 1913. *Dimerosporium ulei* Wint., Hedw. 25:25. 1885. *Dimerosporium paurotrichum* Sacc. and Berl., Rev. Myc. 7. 1885. *Dimerium ulei* Sacc., Syll. Fung. 17:537. 1905. *Dimerosporium oligotrichum* Sacc. and Berl., Rev. Myc. 7. 1885. On *Tibouchina*, Melastomataceae. Ascomata 210-300 μ , asci 65-85 x 42-52 μ , spores 30-33 x 16-17 μ . Broteria 12:81. 1914.

35. CLYPEOLELLA v. Höhnelt

Sitz. K. Akad. Wiss. Wien 119:403. 1910.

Type: *C. inversa*, cf. Theiss., Centralbl. Bakt., Abt. II, 34:229. 1912.

Characters: Free mycelium present, ascomata dimidiate, radiate, no ostiole, no typical paraphyses, spores brown, 2-celled, hyphopodia present, conidia 4-celled.

The original generic description by v. Höhnelt reads "parapen breittfädig." In the same article the type species, *C. inversa*, is given as with typical paraphyses.

1. *Clypeolella ricini* Rac., ap. Theiss., Centralbl. Bakt. 34:233. 1912. *Asteria ricini* Rac., in herb. On *Ricinus*, Euphorbiaceae. Ascomata 50-110 μ , asci 26-28 μ , spores 17-20 x 9-10 μ . Syll. Fung. 24:489.

2. *Clypeolella clermontiae* Stev. and Ryan, Bernice P. Bishop Mus. Bul. 19:72. 1925. On *Clermontia*, Campanulaceae. Ascomata 86-90 μ , asci 36-45 x 27-30 μ , spores 9-13 x 21-19 μ .

3. *Clypeolella inversa* (Sacc. and Trott.) v. Höhn., Sitz. K. Akad. Wiss. Wien 119:403. 1910. *Asterina inversa* Sacc. and Trott., Syll. Fung. 22:544. 1913. On *Maytenus*, Celastraceae. Ascomata 160-270 μ , asci 50-65 x 35-40 μ , spores 22-24 x 10 μ .

4. *Clypeolella solani* Theiss., Centralbl. Bakt. 34:233. 1912. On *Solanum*, Solanaceae. Ascomata 35-55 μ , asci 45-55 x 38-45 μ , spores 25-27 x 10-13 μ . Syll. Fung. 24:489.

5. *Clypeolella leemingii* (E. and E.) Theiss., Centralbl. Bakt. 34:231. 1912. *Asterina leemingii* E. and E., Proc. Acad. Nat. Sci., Philadelphia, p. 128. 1893. On *Galax*, Diapensiaceae. Ascomata 180-250 μ , asci 55-70 x 35-30 μ , spores 28-35 x 11-12 μ . Syll. Fung. 11:256.

6. *Clypeolella stellata* (Speg.) Theiss., Centralbl. Bakt. 34:323. 1912. *Asterina stellata* Speg., Fungi Puigg. no. 358, Acad. Nac. Ci. Cordoba, Bol. 11:567. 1889. On *Weinmannia*, Compositae; Saxifragaceae. Ascomata 120-140 μ , asci 50-62 x 40-48 μ , spores 30-36 x 12-16 μ . Syll. Fung. 9:391; 16:640.

7. *Clypeolella mate* (Speg.) Theiss., Centralbl. Bakt. 34:232. 1912. *Asterina mate* Speg., Ann. Mus. Nac. Buenos Aires Ser. 3, 10:130. 1909; *ibid.* 12:428. 1909. On *Ilex*, Aquifoliaceae. Ascomata 100 μ , asci 50-70 x 40-50 μ , spores 38-40 x 15-18 μ . Syll. Fung. 22:539.

36. TRICHAETERINA Arnaud

Annales de l'École Nationale d'Agriculture Montpellier 16:172. 1918.

Type: *T. styracis* (Theiss.) Arn.

Characters: The same as *Asterina*, but with the mycelium setose; paraphysate.

1. *Trichasterina styracis* (Theiss.) Arn., *l. c.* *Parasterina styracis* Theiss., Ann. Myc. 15:421. 1917. *Asterina styracis* Theiss., Abh. K. K. Zool.-Bot. Ges. 7:41. 1913. *Asterina silvatica* Theiss., Fungi brasil. no. 77, Ann. Myc. 10. 1912. *Asterina silvatica* Rehm, Rick. Fungi Austro-Amer. no. 386. 1905. On *Styrax*, Styraceae. Ascomata 230-300 μ , asci 70-90 x 45-60 μ , spores 30-35 x 19-16 μ . Syll. Fung. 24:477.

37. ASTERINA Lévillé

Ann. Sci. Nat. ser. 3, Bot. 3:59. 1845.

Type: *A. azare* Lév.

Characters: Free mycelium present, hyphopodia or node cells, hymenium simple, ascomata dimidiate, radiate, astomate, circular, spores brown, 2-celled, paraphysate.

Conidial state: *Asterostomella*.

Literature: Abh. K. K. Zool.-Bot. Ges. 7:1-30. 1913; Trans. Roy. Soc. So. Afr. 8:235-282. 1920.

Synonymous genera:

1) *Dimerosporium* Fckl., Symb. Myc. 86. 1869.

2) *Myxasterina* v. Höhn., Sitz. K. Akad. Wiss. Wien 118:870. 1909.

3) *Opeasterina* Speg., Bol. Acad. Nac. Ci. Cordoba 23:498. 1919.

4) *Asterella* Sacc., Myc. Centralbl. 3:274. 1913. Syll. Fung. 9:393.

This genus was described as with hyaline spores. The type, *A. megalo-spora* has brown spores and belongs to *Asterina*. Hyaline spored species are not known. Ann. Myc. 15:424. 1917.

5) *Asterolibertia* Arn., Ann. École Nac. Agr. Montp. 16:165. 1918. Type: *A. coupeiae* (Henn.) Arn. For the present purpose we place this back in the genus *Asterina*.

6) *Anariste* Syd., Ann. Myc. 25:76. 1927. Type: *A. poliothea* Syd. This genus is said by Sydow to differ from *Asterina* in that the asci are embedded in a mucose mass. Instead of hyphopodia it produces characteristic hyphopodia-like branches. The spores are divided early into cells. We here consider it as an *Asterina*.

Theissen recognized three subgenera:

1) *Euasterina*: no basal membrane, paraphyses present. This group now forms the genus *Parasterina*.

2) *Dimerosporium*: no basal membrane, no paraphyses.

3) *Clypeolaster*: basal membrane present, no paraphyses.

The following species are separated as accurately as is possible with the information of published descriptions into the subgenera *Dimerosporium* and *Clypeolaster*. Under each of these the species are arranged in order of maximum spore length.

Sydow in later years has introduced the term "paraphsoides" and has also described "very tenuous basal membranes" which in earlier years would not have been noted. Thus there is doubt in many instances as to allocation to the subgenera.

Subgenus DIMEROSPORIUM Theissen

1. *Asterina effusa* Cke. and Mass., Grev. 15:101. 1886. *Englerula effusa* (Cke. and Mass.) Theiss., Abh. K. K. Zool.-Bot. Ges. 7:24. 1913. On *Pittosporum*, *Pittosporaceae*. Spores $10 \times 5-6 \mu$. Syll. Fung. 9:382. 1891.

2. *Asterina nigerrima* Ellis, Bull. Torr. Bot. Club 7:91. 1881. On *Erigeron*, *Compositae*. Ascomata $75-100 \mu$, asci $30-34 \times 10 \mu$, spores $12 \times 3-4 \mu$. Syll. Fung. 1:48.

3. *Asterina memorae* Henn., Hedw. 43:373. 1904. On *Memora*, *Bignoniaceae*. Ascomata 150μ , asci $30-35 \times 13-17 \mu$, spores $10-13 \times 4.5-5.5 \mu$. Syll. Fung. 17:879; Abh. K. K. Zool.-Bot. Ges. 7:57. 1913. Theissen's key 21.

4. *Asterina ixorae* Ryan, Mycologia 16:182. 1924. On *Ixora*, *Rubiaceae*. Ascomata $168-180 \mu$, asci $12 \times 55 \mu$, spores $12-14 \times 3-5 \mu$.

5. *Asterina aspidii* (Henn.) Theiss., Abh. K. K. Zool.-Bot. Ges. 7:75. 1913. *Asterella aspidii* Henn., Hedw. 43:141. 1904. Syll. Fung. 17:884. *Opeasterina aspidii* Speg., Bol. Akad. Nac. Ci. Cordoba 23:499. 1919. On *Aspidium*, *Pteridophyta*; *Maba*, *Ebenaceae*. Ascomata $50-80 \mu$, asci $25-30 \times 20-25 \mu$, spores $13 \times 7-8 \mu$. Theissen's key 44.

6. *Asterina insignis* Karst. and Roum., Rev. Myc. 12:77. 1890. On Lauraceae. Ascomata 160-200 μ , spores 13-14 x 5-6 μ . Doubtful species. Syll. Fung. 9:384; Abh. K. K. Zool.-Bot. Ges. 7:112. 1913. Theissen's key 95.
7. *Asterina zizphiae* Yates, Philipp. Jour. Sci. 13:375. 1918. On Zizyphus, Rhamnaceae. Ascomata 120-170 μ , asci 40 x 30 μ , spores 15 x 10 μ . Syll. Fung. 24:467.
8. *Asterina lawsoniae* Henn. and Nym., Monsunia 1:159. 1899. *Dimerosporium lawsoniae* Arn., Ann. École Nac. Agr. Montp. 16:179. 1918. On Lawsonia, Lythraceae. Ascomata 80-120 μ , asci 22-30 x 20-26 μ , spores 9-15 x 7-9 μ . Syll. Fung. 16:646; Abh. K. K. Zool.-Bot. Ges. 7:81. 1913. Theissen's key 54.
9. *Asterina dilabens* Syd., Ann. Myc. 2:168. 1904. On Sarmienta, Rhytidophyllum, Gesneria, Gesneriaceae; Solanum, Solanaceae; Tetrazygia, Melastomataceae; Hillia, Rubiaceae. Ascomata 90-200 μ , asci 22-26 x 18-24 μ , spores 12-15 x 7-9 μ . Syll. Fung. 17:879; Mycologia 16:181. 1924; Abh. K. K. Zool.-Bot. Ges. 7:90. 1913; N. Y. Acad. Sci. 8:18. 1926. Theissen's key 66.
10. *Asterina undulata* Doidge, Trans. Roy. Soc. So. Afr. 8:258. 1920. On Viola, Violaceae. Near *A. veronicae*. Asci 20-24 x 17-20 μ , spores 13-15 x 6-8.5 μ . Doidge's key 21.
11. *Asterina hians* Syd., Ann. Myc. 14:91. 1916. On Dioscorea, Dioscoreaceae. Ascomata 65-90 μ , asci 25-35 x 24-29 μ , spores 14-16 x 6-7 μ . Syll. Fung. 24:450.
12. *Asterina gouldiae* Stev. and Ryan, Bernice P. Bishop Mus. Bul. 19:73. 1925. On Gouldia, Rubiaceae. Ascomata 145-240 μ , asci 63-72 x 27-39 μ , spores 7 x 16 μ .
13. *Asterina derridis* Henn., Hedw. 47:260. 1908. On Derris and Pongamia, Leguminosae. Ascomata 70-90 μ , asci 20-30 x 20-25 μ , spores 11-16 x 6-8 μ . Syll. Fung. 22:538; Abh. K. K. Zool.-Bot. Ges. 7:78. 1913. Theissen's key 47.
14. *Asterina circularis* Wint. (not Pat.), Hedw. 25:94. 1886. On leaves. Asci 36-44 x 23-30 μ , spores 15-16 x 8-9 μ . Syll. Fung. 9:388.
15. *Asterina balansae* Speg., Bol. Acad. Nac. Ci. Cordoba 11:559. 1889. *Asterina balansae* (Speg.) Theiss., Abh. K. K. Zool.-Bot. Ges. 7:88. 1913. *Asterina balansae* (Speg.) Sacc. and Trott., Syll. Fung. 22:537. 1913. *Seynesia balansae* Speg. Fungi Guar. I, no. 297; II, no. 130; Syll. Fung. 9:1065. 1891. On Myrtaceae; Ildefonsia, Scrophulariaceae. *Var. macrospora* Theiss. (not Speg.), Abh. K. K. Zool.-Bot. Ges. 7:88. 1913. On Leguminosae. *Var. africana* Sacc., Hedw. 37:133. 1899. Syll. Fung. 16:640; Ann. Myc. 10:24. 1912. On Rubus, Rosaceae. Ascomata 100-150 μ , asci 40 x 28 or 28-45 x 18-24 μ , spores 18-22 x 8-10 μ . Syll. Fung.

14:689; Trans. Roy. Soc. So. Afr. 8:257. 1920; Öst. Bot. Ges. 62:435. 1912; Hedw. 37:327. 1898. "Nicht zu verwechseln ist die Art mit der chinesischen *Asterina balansae* Karst. und Roum. — *Asterina balanseana* K. and R. = *Asterostomella balanseana* (K. and R.) Theiss., Frag. brasil. no. 152." Theissen (86) lists 25 collections which are wrongfully called *Asterina balansae*. Four forms of *Seynesia balansae* were designated and should be regarded as forms of *Asterina balansae*. They are as follows:

1) Form *Solani verbascifolii*, Syll. Fung. 9:1065. On Solanum, Solanaceae. Ascomata 100-120 μ , asci 30 x 20-25 μ , spores 10 x 8 μ .

2) Form *Macluræ*, Syll. Fung. 9:1065. On Maclura, Moraceae. Ascomata 80-100 μ , asci 30 x 25 μ , spores 15 x 7 μ .

3) Form *Solani*, Syll. Fung. 9:1065. On Solanum, Solanaceae. Ascomata 150-200 μ , asci 35-40 x 25-32 μ , spores 14-16 x 7-8 μ .

4) Form *Acanthacearum*, Syll. Fung. 9:1065. On Acanthaceae. Ascomata 60-70 μ , asci 25-30 x 20-22 μ , spores 15 x 7-8 μ .

16. *Asterina gerbericola* Doidge, Bothalia 2:202. 1927. On Gerbera, Compositae. Ascomata 120-130 μ , asci 20-23 x 23-30 μ , spores 13.5-16.5 x 7-8.3 μ .

17. *Asterina natalensis* Doidge, Trans. Roy. Soc. So. Afr. 8:248. 1920. On Mikania, Compositae. Ascomata 120-130 μ , asci 26-32 x 20-24 μ , spores 13-17 x 8-10 μ .

18. *Asterina simillima* Syd., Ann. Myc. 15:242. 1917. On Luffa, Curcubitaceae. Ascomata 80-115 μ , asci 25-30 x 20-24 μ , spores 14-17 x 6-7.5 μ . Syll. Fung. 24:448.

19. *Asterina ildefonsiae* (Rehm) Theiss., Abh. K. K. Zool.-Bot. Ges. 7:87. 1913. *Seynesia balansae* Speg. var. *ildefonsiae* Rehm, Hedw. 35:101. 1895. Syll. Fung. 14:689. On Claoxylon, Euphorbiaceae; Ildefonsia, Scrophulariaceae; Melothria, Cucurbitaceae. *Asterella gardoquiae* Syd., Ann. Myc. 2:169. 1904. Syll. Fung. 17:883. On Gardoquia, Labiatae. Ascomata 80-120 μ , asci 27-32 x 25-28 μ , spores 14-17 x 6.5-8 μ . Theissen's key 62.

20. *Asterina veronicae* (Lib.) Cooke, Grev. 5:112. 1876. *Dimerosporium veronicae* Fckl., v. Höhn., Frag. zur Myk. no. 477. *Dothidea veronicae* Lib., Pl. crypt. Arduenna. II, no. 173. 1832. *Sphaeria abjecta* Wallr., Flora crypt. part II, p. 810. 1833. *Dimerosporium abjectum* (Wallr.) Fckl., Symb. Myc. p. 89. 1869. *Dimerosporium abjectum* (Lib. par erreur) Fckl., Syll. Fung. 1:51. 1882, et auteurs divers. *Meliola abjecta* (Wallr.) Schröter, Tab. f. europei no. 2424. *Asteroma veronicae* Desm., Pl. Crypt., ed. I, fasc. XVI, 1836, no. 788, with figures and description. Ed. II, fasc. IV, 1839, no. 180. (Pour la ferme pycnide). *Asteroma veronicae* Desm. in Marchal (Crypt. belg. 76.) *Dimerosporium veronicae* Arn., Ann. École Nac. Agr. Montp. 16:174. 1918. *Asteroma veronicarum*

Rahb., Herb. Myc., ed. II, no. 739; and in Fckl., F. rhen. no. 461. *Capnodium sphaericum* Cooke, Handb. Brit. Fung., II, no. 2808. 1871. On Veronica, Scrophulariaceae. Ascomata 90-150 μ , asci 32-40 x 16-20 μ , spores 15-17 x 6.5-8 μ . Syll. Fung. 1:51; Abh. K. K. Zool.-Bot. Ges. 7:87. 1913. Theissen's key 63.

21. *Asterina eupomatiae* Henn., Hedw. 42:78. 1903. On Eupomatia, Anonaceae. Ascomata 60 μ , asci 25-30 x 22-28 μ , spores 12-18 x 5-6 μ . Syll. Fung. 17:882; Abh. K. K. Zool.-Bot. Ges. 7:64. 1913. *Var dalechampia* Theiss., Abh. K. K. Zool.-Bot. Ges. 7:64 1913. On Dalechampia, Euphorbiaceae. Theissen's key 29.

22. *Asterina lobata* Syd., Leaflet Philipp. Bot. 5:1541. 1912; *ibid.* 6:1927. 1913. On Picrasma, Simarubaceae. Ascomata 90-125 μ , asci 25-35 x 20-25 μ , spores 13-18 x 6-7 μ . Syll. Fung. 24:472; Abh. K. K. Zool.-Bot. Ges. 7:119. 1913. Theissen's key 116.

23. *Asterina negeriana* Syd., Ann. Myc. 2:167. 1904. On Escallonia, Saxifragiaceae. Ascomata 100-175 μ , asci 25-35 x 18-28 μ , spores 14-18 x 7-7.5 μ . Syll. Fung. 17:877; Abh. K. K. Zool.-Bot. Ges. 7:90. 1913. Theissen's key 65.

24. *Asterina raripoda* Doidge, Trans. Roy. Soc. So. Afr. 8:254. 1920. On Ansellia, Orchidaceae. Ascomata 150-200 μ , asci 40-52 x 16-24 μ , spores 15-18 x 7-10 μ .

25. *Asterina strychni* v. Höhn., Sitz. K. Akad. Wiss. Wien 118:868. 1909; Abh. K. K. Zool.-Bot. Ges. 7:61. 1913. *Myxasterina strychni* v. Höhn., Sitz. K. Akad. Wiss. Wien 118:868. 1909. On Strychnos, Loganiaceae. Asci 40-50 x 18 μ , spores 12-16 x 5-6 μ . Theissen's key 27.

26. *Asterina lobulifera* Syd., Philipp. Jour. Sci. 9:181. 1914. On Glochidion, Euphorbiaceae. Ascomata 100-140 μ , asci 25-30 x 20-25 μ , spores 16-18 x 7-8.5 μ . Syll. Fung. 24:454.

27. *Asterina streptocarpi* Doidge, Bothalia 2:203. 1927. On Streptocarpus, Gesneriaceae. Ascomata 100-150 μ , asci 20-24 x 23-24 μ , spores 16-18 x 7-8.5 μ .

28. *Asterina kauaiensis* Stev. and Ryan, Bernice P. Bishop Mus. Bul. 19:73. 1925. On unknown host. Ascomata 144 μ , asci 32-36 μ , spores 18 x 9 μ .

29. *Asterina suttoniae* Stev. and Ryan, Bernice P. Bishop Mus. Bul. 19:74. 1925. On Suttonia, Myrsinaceae. Ascomata 79-384 μ , spores 18 x 9 μ .

30. *Asterina piperina* Syd., Ann. Myc. 15:243. 1917. *Asterina piperis* Yates, Philipp. Jour. Sci. 13:374. 1918. On Piper, Piperaceae. Ascomata 100-175 μ , asci 25-35 x 18-28 μ , spores 14-18 x 7-8.5 μ . Abh. K. K. Zool.-Bot. Ges. 7:90. 1913. Theissen's key 65.

31. *Asterina portoricensis* Ryan, Mycologia 16:185. 1924. On

Solanum, Solanaceae. Ascomata 72-84 μ , asci 19-21 x 19-29 μ , spores 17-19 x 7 μ .

32. *Asterina myrciae* Ryan, Mycologia 16:186. 1924. On *Eugenia* and *Myrcia*, Myrtaceae. Ascomata 108-116 μ , asci 12-19 x 21-24 μ , spores 19 x 7 μ .

33. *Asterina theissenia* Ryan, Mycologia 16:187. 1924. On *Miconia*, Melastomataceae. Ascomata 168-265 μ , asci 24 x 38 μ , spores 19 x 9 μ .

34. *Asterina ocotearum* Petr. and Cif., Ann. Myc. 30:162. 1932. On *Ocotea*, Lauraceae. Ascomata 80-180 μ , asci 25-38 x 20-32 μ , spores 15-20 x 7-9.5 μ .

35. *Asterina dictyolomatis* Henn., Hedw. 43:372. 1904. On *Dictyoloma*, Rutaceae. Ascomata 100-150 μ , asci 30-40 x 30 μ , spores 15-20 x 8-10 μ . Syll. Fung. 17:877; Abh. K. K. Zool.-Bot. Ges. 7:71. 1913. Theissen's key 36.

36. *Asterina cassiae* Syd., Philipp. Jour. Sci. 8:275. 1913. On *Glochidion*, Euphorbiaceae; *Cnestis*, Connaraceae. Ascomata 100-140 μ , asci 26-34 x 22-28 μ , spores 16-20 x 6-7 μ . Syll. Fung. 24:453; Ann. Myc. 21:103. 1923.

37. *Asterina singaporensis* Syd., Ann. Myc. 18:159. 1920. On *Derris sinnata*, Leguminosae. Ascomata 80-110 μ , asci 30-40 x 20-24 μ , spores 16-20 x 6-8 μ . Syll. Fung. 24:457.

38. *Asterina pusilla* Syd., Philipp. Jour. Sci. 8:488. 1913. On *Premna*, Verbenaceae. Ascomata 70-80 μ , asci 20-26 x 17-20 μ , spores 16-20 x 7-8 μ . Syll. Fung. 24:474.

39. *Asterina decipens* Syd., Leaflet Philipp. Bot. 5:1540. 1912. On *Champereia*, Santalaceae. Ascomata 120-170 μ , asci 15-25 x 12-18 μ , spores 16-20 x 8-9 μ . Syll. Fung. 24:470; Abh. K. K. Zool.-Bot. Ges. 7:118. 1913. Theissen's key 114.

40. *Asterina tenella* Cooke, Grev. 13:87. 1855. *Asterina delitescens* Ell. and Mart., Amer. Natur. 17:1381. 1883. On *Persea*, Lauraceae; *Vaccinium*, Ericaceae. Ascomata 100-140 μ , asci 25-32 μ , spores 16-20 x 8-10 μ . Syll. Fung. 9:383; Abh. K. K. Zool.-Bot. Ges. 7:76. 1913; Bernice P. Bishop Mus. Bul. 19:74. 1925. Theissen's key 45.

41. *Asterina flacourtiae* Petr., Ann. Myc. 29:225. 1931. On *Flacourtia*, Flacourtiaceae. Ascomata 150-250 μ , asci 60-80 μ , spores 17-20 μ .

42. *Asterina confertissima* Syd., Ann. Myc. 14:90. 1916. On *Arthrostemma*, Melastomataceae. Ascomata 120-160 μ , asci 35-50 x 18-26 μ , spores 17-20 x 8-10 μ .

43. *Asterina crotoniensis* (Doidge) Ryan, n. name. *Asterina crotonicola* Doidge, Bothalia 1:76. 1921. (Name preempted by *A. crotonicola* Pat.) On *Croton*, Euphorbiaceae. Ascomata 120-140 μ , asci 36-40 x 23-33 μ , spores 17-20 x 12-13 μ .

44. *Asterina perconferta* Trott., Syll. Fung. 24:466. 1926. *Asterina confertissima* Speg., Bol. Acad. Nac. Ci. Cordoba 23:572. 1919. On Passiflora, Passifloraceae. Ascomata 80-120 μ , asci 38-40 x 25-30 μ , spores 18-20 μ .

45. *Asterina pipturi* Syd., Ann. Myc. 14:366. 1916. On Pipturus, Urticaceae. Ascomata 80-100 μ , asci 25-35 x 22-30 μ , spores 18-20 x 7-8 μ . Syll. Fung. 24:474. Theissen's key 54.

46. *Asterina perpusilla* Syd., Ann. Myc. 14:366. 1916. On Alangium, Cornaceae. Ascomata 70-160 μ , asci 25-30 x 20-22 μ , spores 18-20 x 9-11 μ . Syll. Fung. 24:448.

47. *Asterina ekmanii* Petr. and Cif., Ann. Myc. 30:158. 1932. On Gonzalea, Rubiaceae. Ascomata 140-200 μ , asci 35-40 x 20-28 μ , spores 17-21 x 6.5-8 μ .

48. *Asterina delicatula* Syd. and Bal., Ann. Myc. 19:308. 1921. On Aegle, Rutaceae. Ascomata 90-120 μ , asci 30-40 x 25-30 μ , spores 18-20 x 8-10 μ .

49. *Asterina mitrariae* Syd., Ann. Myc. 29:86. 1931. On Mitraria, Gesneriaceae. Ascomata 120-200 μ , asci 30-37 x 25-32 μ , spores 15-21 x 10-11 μ .

50. *Asterina sydowiana* Ryan, Mycologia 16:184. 1924. On Chrysophyllum and Micropholis, Sapotaceae. Ascomata 112-224 μ , asci 19-31 x 36-38 μ , spores 9 x 21 μ . N. Y. Acad. Sci. 8:20. 1926.

51. *Asterina grammocarpa* Syd., Ann. Myc. 12:557. 1914. On Symplocus, Symplocaceae. Ascomata 90-120 μ , spores 17-22 x 8-9 μ . Syll. Fung. 24:473.

52. *Asterina clermontiae* Stev. and Ryan, Bernice P. Bishop Mus. Bul. 19:73. 1925. On Clermontia, Campanulaceae. Ascomata 90-180 μ , asci 21-32 x 36-45 μ , spores 9-18 x 16-21 μ .

53. *Asterina phaleriae* Mendoza, Philipp. Jour. Sci. 49:185. 1932. On Leucosyke, Urticaceae. Ascomata 80-120 μ , asci 30-35 x 25-31 μ , spores 17-22 x 9-10 μ .

54. *Asterina crebra* Syd., Ann. Myc. 11:327. 1913. On Opilia, Opiliaceae. Ascomata 90-125 μ , asci 27-38 x 20-30 μ , spores 18-22 x 7-9 μ . Syll. Fung. 24:463.

55. *Asterina rickii* Theiss., Abh. K. K. Zool.-Bot. Ges. 7:69. 1913. *Seynesia* ? *paraguayensis* Theiss., Fung. Bras. no. 68, Ann. Myc. 10. 1912. On Myrtaceae. Ascomata 100-150 μ , asci 35-40 x 38-30 or 50 x 32 μ , spores 18-22 x 8-9 μ . Theissen's key 34.

56. *Asterina balii* Syd., Ann. Myc. 19:308. 1921. On Alangium, Cornaceae. Ascomata 100-130 μ , asci 30-40 x 25-35 μ , spores 18-22 x 8-10 μ .

57. *Asterina ampullulipeda* Speg., Fungi Guar. no. 127, Rev. Myc. 9.

1887. On *Nectandra*, Lauraceae. Ascomata 100-120 μ , asci 40 x 30 μ , spores 19-22 x 8-9 μ . Abh. K. K. Zool.-Bot. Ges. 7:68. 1913. Syll. Fung. 9:382. 1891. Theissen's key 33.

58. *Asterina liparidis* Rac., Abh., K. K. Zool.-Bot. Ges. 7:91. 1913. On *Liparis*, Orchidaceae. Ascomata 150-220 μ , or 250 x 150 μ , asci 30-38 x 25-30 μ , spores 19-22 x 8-10 μ . Syll. Fung. 24:464. Theissen's key 67.

59. *Asterina banguiensis* Yates, Philipp. Jour. Sci. 13:372. 1918. On *Glycosmis*, Rutaceae. Ascomata 120-160 μ , asci 45-50 x 18-22 μ , spores 20-22 x 8-10 μ . Syll. Fung. 24:469.

60. *Asterina delicata* Doidge, Trans. Roy. Soc. So. Afr. 8:253. 1920. On *Trimeria*, Flacourtiaceae. Ascomata 100-130 μ , asci 26-33 x 33-40 μ , spores 20-22 x 10-12 μ . Doidge's key 9.

61. *Asterina quarta* Rac., Abh. K. K. Zool.-Bot. Ges. 7:77. 1913. On *Syzygium*, Myrtaceae. Ascomata 200-300 μ , asci 75-85 x 30-40 μ , spores 20-22 x 11-14 μ . Syll. Fung. 24:462. Theissen's key 46.

62. *Asterina triumfettae* (Arn.) Stev., n. comb. *Dimerosporium triumfettae* Arn., Ann. École Nat. Agr. Montp. 16:180, tab. 36. 1918; Bull. Soc. Myc. Fr. 36:39. 1920. On *Triumfetta*, Tillaceae. Ascomata 60-100 μ , asci 30-40 μ , spores 18-23 x 10-12 μ . Syll. Fung. 24:478. 1926.

63. *Asterina venustula* Syd., Philipp. Jour. Sci. 21:140. 1922. On *Averrhoa*, Oxalidaceae. Ascomata 150-175 μ , asci 32-40 x 25-30 μ , spores 20-23 x 8-9 μ .

64. *Asterina scolopiae* Doidge, Bothalia 1:77. 1920. On *Scolopia*, Flacourtiaceae. Ascomata 150-170 μ , asci 33-40 μ , spores 20-23.5 x 9-11 μ .

65. *Asterina secamonicola* Doidge, Bothalia 2:235. 1927. On *Secamone*, Asclepiadaceae. Ascomata 200-240 μ , asci 40-50 x 24-27 μ , spores 20-23 x 9-10 μ .

66. *Asterina laxa* Wint., Hedw. 31:102. 1892. On unknown host. Ascomata 80-120 μ , asci 43-48 x 23-30 μ , spores 22-23 x 9-10 μ . Syll. Fung. 11:256; Abh. K. K. Zool.-Bot. Ges. 7:78. 1913. Theissen's key 48.

67. *Asterina miconiae* Ryan, Mycologia 16:181. 1925. (Not *A. miconiae* Theiss.) *Asterina spathulata* Seav. and Char., N. Y. Acad. Sci. 8:20. 1926. On *Miconia*, Melastomataceae. Ascomata 168-201 μ , asci 41-48 x 9 μ , spores 19-24 x 5-7 μ .

68. *Asterina silvatica* Speg., Fungi Puigg. no. 359, Bol. Acad. Nac. Ci. Cordoba 11. 1889. On *Trichilia*, Meliaceae. Asci. 40-55 x 25-30 μ , spores 20-24 x 8-10 μ . Theissen's key 50.

69. *Asterina combreti* Syd., Engl. Bot. Jahrb. 45:264. 1910. On *Combretum*, Combretaceae. Ascomata 130-170 μ , asci 35-45 x 32-40 μ , spores 20-24 x 9-11 μ . *Var. kutuensis* (Henn.) v. Höhn. *Hyphaster kutensis* Henn., in H. Baum, Ber. der Kunene-Zambesi-Exped. p. 169.

1902. *Asterina (Dimerosporium) kutuensis* v. Höhn., Frag. zur Myk. XII, no. 599. On Combretum, Combretaceae. *Var. brasiliensis* Theiss., Abh. K. K. Zool.-Bot. Ges. 7:63. 1913. *Asterina combreti* var. *brasiliana* Speg., Ann. Mus. Nac. Buenos Aires 23:504. 1919. On Acanthaceae. Syll. Fung. 24:447. 1926; Trans. Roy. Soc. So. Afr. 8:249. 1920. Theissen's key 28.

70. *Asterina spissa* Syd., Ann. Myc. 9:392. 1911. *Dimerosporium spissum* Arn., Ann. École Nat. Agr. Montp. 16:178. 1918. On Jasminum, Oleaceae. Ascomata 130-170 μ , asci 38-45 x 30-35 μ , spores 20-24 x 9-12 μ . Syll. Fung. 24:464; Abh. K. K. Zool.-Bot. Ges. 7:61. 1913. Theissen's key 26.

71. *Asterina sphaerasca* Thüem., F. Austro-Africo 119. 1878. On Capparis, Capparidaceae. Ascomata 130-170 μ , asci 35-45 μ , spores 20-24 x 10-12 μ . Doubtful species. Syll. Fung. 1:40. 1882; Abh. K. K. Zool.-Bot. Ges. 7:115. 1913; Trans. Roy. Soc. So. Afr. 8:262. 1920.

72. *Asterina tropicalis* Speg., Ann. Mus. Nac. Buenos Aires 23:211. 1912. On Rheedea, Guttiferae. Ascomata 120-150 μ , asci 45-50 x 35 μ , spores 24 x 12 μ . Syll. Fung. 24:449.

73. *Asterina mappiae* Petr. and Cif., Ann. Myc. 28:279. 1930. On Mappia, Icacinaceae. Ascomata 80-150 μ , asci 38-45 μ , spores 20-24 x 10-12.5 μ .

74. *Asterina oligocarpa* Syd., Ann. Myc. 12:558. 1914. On Olax, Olacaceae. Ascomata 50-70 μ , asci 40-45 x 30-35 μ , spores 20-24 x 15-18 μ . Syll. Fung. 24:463.

75. *Asterina cinnamomi* Syd., Ann. Myc. 21:103. 1923. On Cinnamomum, Lauraceae. Ascomata 100-150 μ , asci 35-42 x 22-32 μ , spores 22-24 x 10-12 μ .

76. *Asterina libertiae* Syd., Ann. Myc. 2:167. 1904. *Asterina leveillei* Pat., Jour. Bot. 26:148. 1888. On Libertia, Iridaceae; Arundo, Gramineae. Ascomata 140-200 μ , asci 42 x 28-38 μ , spores 18-25 x 9-11 μ . Syll. Fung. 9:387; 17:880; Abh. K. K. Zool.-Bot. Ges. 7:81. 1913. Theissen's key 55.

77. *Asterina coccolobae* Ferd. and Winge, Botan. Tidsskr. 29:10, tab. 1, fig. 2. 1908. On Coccoloba, Polygonaceae. Ascomata 175-350 μ , asci 38-50 x 25-37 μ , spores 20-25 x 8-11 μ . Syll. Fung. 22:543.

78. *Asterina breyniae* Syd., Ann. Myc. 15:242. 1917. *Asterina breyniaecola* Trott., Syll. Fung. 24:452. On Breynia, Euphorbiaceae. Ascomata 150-250 μ , asci 45-55 x 30-38 μ , spores 21-25 x 10-11 μ . Syll. Fung. 24:452; Ann. Myc. 20:72. 1922.

79. *Asterina trachycarpa* Syd., Leaflet Philipp. Bot. 5:1542. 1912. On Derris, Leguminosae. Ascomata 125-180 μ , asci 30-40 x 22-26 μ , spores

20-25 x 10-11 μ . Syll. Fung. 24:456; Abh. K. K. Zool.-Bot. Ges. 7:119. 1913. Theissen's key 118.

80. *Asterina crotonis* Syd., Ann. Myc. 14:91. 1916. On Croton, Euphorbiaceae. Ascomata 150-200 μ , asci 45-50 x 30-40 μ , spores 20-25 x 9-12 μ . Syll. Fung. 24:453.

81. *Asterina ditissima* Syd., Ann. Myc. 15:243. 1917. On Eugenia, Myrtaceae. Ascomata 200-320 μ , asci 50-64 x 20-28 μ , spores 22-25 x 10-12 μ . Syll. Fung. 24:462.

82. *Asterina hendersoni* Doidge, Trans. Roy. Soc. So. Afr. 8:255. 1920. On Ilex, Aquifoliaceae. Ascomata 150-200 μ , asci 45-50 x 26-33 μ , spores 23-25 μ . Doidge's key 15.

83. *Asterina rhamnicola* Doidge, Trans. Roy. Soc. So. Afr. 8:255. 1920. On Rhamnus, Rhamnaceae. Ascomata 225-280 μ , asci 45-50 x 23-33 μ , spores 23-25 x 9-12 μ . Doidge's key 14.

84. *Asterina pulla* Lév., Ann. Sci. Nat. 3:60. 1845. On Melastomataceae. Ascomata 180-240 μ , asci 50-75 x 26-30 μ , spores 23-26 x 8-10 μ . Syll. Fung. 1:51; Abh. K. K. Zool.-Bot. Ges. 7:88. 1913. Theissen's key 52.

85. *Asterina punctiformis* Lév., Ann. Sci. Nat. 4:267. 1846. On Conceveiba, Euphorbiaceae; Gesneria, Gesneriaceae. Ascomata 120-150 μ , asci 38-43 x 30-35 μ , spores 22-26 x 10-12 μ . *Var. fimbriata*. *Asterina fimbriata* Kalch. and Cke., Grev. 9:138. 1880. Syll. Fung. 1:41. *Sclerochiton harveyanum* Kalch. no. 1290, auf Hypoestes Wood 608, Sudafrica, herb. Kew. On Sclerochiton, Acanthaceae. Mycologia 16:186; Abh. K. K. Zool.-Bot. Ges. 7:66. 1913; Trans. Roy. Soc. So. Afr. 8:251. 1920. Theissen's key 31.

86. *Asterina indica* Syd., Ann. Myc. 9:390. 1911. On Symplocus, Symplocaceae. Ascomata 150-200 μ , asci 43-62 x 30-40 μ , spores 22-26 x 10-13 μ . Syll. Fung. 24:473; Abh. K. K. Zool.-Bot. Ges. 7:86. 1913. Theissen's key 61.

87. *Asterina hoveaefolia* Cke. and Mass., Grev. 22:36. 1893. On Hovea, Leguminosae. Ascomata 200-250 μ , asci 50 x 36-45 μ , or 62-72 x 30-35 μ , spores 23-26 x 10-12 μ . Syll. Fung. 11:255; Abh. K. K. Zool.-Bot. Ges. 7:80. 1913. Theissen's key 51.

88. *Asterina ferruginosa* Doidge, Trans. Roy. Soc. So. Afr. 8:254. 1920. On Cussonia, Araliaceae. Ascomata 160-190 μ , asci 33-37 μ , spores 23-26 x 11-12.5 μ . Doidge's key 13.

89. *Asterina densa* Syd., Ann. Myc. 12:557. 1914. On Pittosporum, Pittosporaceae. Ascomata 170 μ , asci 40-55 x 35-40 μ , spores 24-26 x 9-10 μ . Syll. Fung. 24:467.

90. *Asterina sphaeropoda* Syd., Ann. Myc. 15:242. 1917. On Ostodes, Euphorbiaceae. Ascomata 160-200 μ , asci 50-60 x 30-35 μ , spores 24-26 x 10-13 μ . Syll. Fung. 24:454.

91. *Asterina assimilis* Syd., Philipp. Jour. Sci. 21:140. 1922. On *Eugenia*, Myrtaceae. Ascomata 200-300 μ , asci 60-80 x 30-40 μ , spores 24-26 x 13-15 μ .

92. *Asterina melastomacearum* Ryan, Mycologia 16:186. 1924. On *Miconia*, Melastomataceae. Ascomata 168-268 μ , asci 43 x 53-62 μ , spores 14-26 μ .

93. *Asterina uribei* Toro, Jour. Dept. Agr. Puerto Rico 13:231. 1930. On *Miconia*, Melastomataceae. Ascomata 160-200 μ , asci 65-68 x 24-27 μ , spores 24-27 x 10-13 μ .

94. *Asterina excoecariae* Doidge, Trans. Roy. Soc. So. Afr. 8:258. 1920. On *Excoecaria*, Euphorbiaceae. Ascomata 100-120 μ , asci 35-40 μ , spores 23-27 x 12-13.5 μ . Doidge's key 20.

95. *Asterina trichiliae* Doidge, Trans. Roy. Soc. So. Afr. 8:253. 1920. On *Trichilia*, Meliaceae. Ascomata 190-220 μ , asci 40-46 x 43-50 μ , spores 25-27 x 12-13 μ .

96. *Asterina nothopegiae* Ryan, Mem. Dept. Agr. India 15:104. 1927. On *Nothopegia*, Anacardiaceae. Ascomata 132-181 μ , asci 20-33 x 25-42 μ , spores 8-10 x 20-28 μ .

97. *Asterina kernii* Toro, Mycologia 17:133. 1925. On *Brunellia*, Brunelliaceae. Ascomata 132-208 μ , asci 42-56 x 35-46 μ , spores 21-28 x 14 μ . N. Y. Acad. Sci. 8:19. 1926.

98. *Asterina peglerae* Doidge, Trans. Roy. Soc. So. Afr. 8:250. 1920. On *Rhus* (?), Anacardiaceae. Ascomata 100-160 μ , asci 45-50 x 43-45 μ , spores 23-28 x 15-16.5 μ . Doidge's key 6.

99. *Asterina correicola* Cke. and Mass., Grev. 16:5. 1887. On *Correa*, Rutaceae; *Miconia*, Melastomataceae. Ascomata 200-250 or 300 x 220 μ , asci 42-65 x 32-42 μ , spores 24-28 x 10-10.5 μ . "Die Art weicht von *A. aucubae* durch derbere Myzelhyphen und kleinere Sporen ab; *A. guaranitica* hat bedeutend sterkere Sporen und etwas schwachere Hyphopodien." Syll. Fung. 9:383; Abh. K. K. Zool.-Bot. Ges. 7:92. 1913. Theissen's key 68.

100. *Asterina opposita* Syd., Leaflet Philipp. Bot. 6:1926. 1913. On Meliaceae. Ascomata 120-175 μ , asci 42-52 x 30-40 μ , spores 24-28 x 12-14 μ . Syll. Fung. 24:461.

101. *Asterina gibbosa* Gaill., Bul. Soc. Myc. Fr. 13:180. 1897. On leaves of unknown host; on *Randia* and *Basanacantha*, Rubiaceae. Ascomata 50-90 μ , asci 27-32 x 18-24 μ , spores 16-20 x 8-9 μ . Syll. Fung. 14:697; Abh. K. K. Zool.-Bot. Ges. 7:57. 1913. *Var. megathyria* Doidge, Trans. Roy. Soc. So. Afr. 8:248. 1920. On *Tricalysia*, *Randia*, *Pavetta*, *Alberta* ?, *Plectronia*, Rubiaceae. Ascomata 140-200 μ , asci 33-34 x 27-33 μ , spores 16-20 x 8-9 μ . Theissen's key 20.

102. *Asterina opaca* Syd., Ann. Myc. 10:38 1912. On *Chrysophyllum*,

Sapotaceae. Ascomata 150-250 μ , asci 50-70 x 35-46 μ , spores 26-28 x 13-14 μ . Very near *A. sphaerotheca*, dubious species. Syll. Fung. 24:470; Abh. K. K. Zool.-Bot. Ges. 7:113. 1913; Trans. Roy. Soc. So. Afr. 8:255. 1920. Theissen's key 98.

103. *Asterina henningsii* (Henn.) Theiss., Frag. brasil. no. 78, Ann. Myc. 10:6. 1912. *Asterina solanicola* Henn. (not B. and C.), Hedw. 41:108. 1902. *Dimerosporium henningsii* Arn., Ann. École Nat. Agr. Montp. 16:176. 1918. On Solanum, Solanaceae. Ascomata 80-120 μ , asci 48-65 x 36-56 μ , spores 25-29 x 12-13 μ . Syll. Fung. 17:879; Abh. K. K. Zool.-Bot. Ges. 7:65. 1913. Theissen's key 30.

104. *Asterina plectroniaecola* Mendoza, Philipp. Jour. Sci. 49:187. 1932. On Plectronia, Rubiaceae. Ascomata 80-160 μ , asci 35-41 x 28-35 μ , spores 26-29 x 10-13 μ .

105. *Asterina echinospora* v. Höhn., Sitz. K. Akad. Wiss. Wien 118:440. On Casjera, Opiliaceae. Ascomata 150-240 μ , asci 44-48 x 36 μ , spores 26-29 x 12-14 μ . Syll. Fung. 22:539; Abh. K. K. Zool.-Bot. Ges. 7:72. 1913. Theissen's key 38.

106. *Asterina elmeri* Syd., Leaflet Philipp. Bot. 4:1156. 1911. On Champereia, Santalaceae. Ascomata 120-180 μ , asci 40-50 x 30-45 μ , spores 25-30 x 10-14 μ . Syll. Fung. 24:479; Abh. K. K. Zool.-Bot. Ges. 7:58. 1913; Ann. Myc. 21:103. 1923. Theissen's key 22.

107. *Asterina dispar* Speg., Fungi Puig., Bol. Acad. Nac. Ci. Cordoba 11:562. 1889. On Styrax, Styraceae. Ascomata 180-200 μ , asci 45-50 μ , spores 25-30 x 12-14 μ . Syll. Fung. 9:384. 1891. Theissen's key 42.

108. *Asterina melanomera* Syd., Ann. Myc. 15:241. 1917. On Dasymaschalon, Anonaceae. Ascomata 180-240 μ , asci 35-50 x 30-40 μ , spores 25-30 x 12-14 μ . Syll. Fung. 24:443; Ann. Myc. 21:103. 1923.

109. *Asterina couepiae* Henn., Hedw. 34:104. 1895. *Seynesia heteropteridis* Theiss., Broteria 8:10. 1910. *Asterolibertia couepiae* Arn., Ann. École Nat. Agr. Montp. 16:166. 1918. On Couepia, Rosaceae. Ascomata 200-250 μ , asci 40-50 μ , spores 26-30 x 9-13 μ . Syll. Fung. 22:523; Abh. K. K. Zool.-Bot. Ges. 7:56. 1913. Theissen's key 18.

110. *Asterina elaeocarpi* Syd., Leaflet Philipp. Bot. 4:1156. 1911. On Elaeocarpus, Elaeocarpaceae; Herpetica, Cassia, Leguminosae. Ascomata 100-180 μ , asci 42-60 x 28-35 μ , spores 26-30 x 10-13 μ . Syll. Fung. 24:452; Abh. K. K. Zool.-Bot. Ges. 7:73. 1913; N. Y. Acad. Sci. 8:9. 1926. Theissen's key 40.

111. *Asterina bellucia* Henn., Hedw. 43:374. 1904. *Asterina racemosae* Ryan, Mycologia 16:182. 1924. *Asterina miconicola* Ryan, Mycologia 16:182. 1924. On Miconia and Bellucia, Melastomataceae. Ascomata 100-135 μ , asci 46 x 54 μ , spores 26-30 x 11-13 μ . Jour. Dept. Agr. Puerto Rico 13:229. 1929; Abh. K. K. Zool.-Bot. Ges. 7:72. 1913; Ann. Myc. 27:54. 1929. Theissen's key 39.

112. *Asterina megalocarpa* Berk. and Curtiss, U. S. North Pacific Explor. Exped., Amer. Jour. Sci. 11:129. 1851. Syll. Fung. 1:42; (Sub megalospora) Herb. of the U. S. North Pacific Explor. Exped. no. 168. On leaves. Ascomata 250 μ , asci 55-68 x 40-52 μ , spores 26-30 x 11-13 μ . Abh. K. K. Zool.-Bot. Ges. 7:75. 1913. Thiessen's key 43.

113. *Asterina holarrhenae* Ryan, Mem. Dept. Agr. India 15:103. 1927. On *Holarrhena*, Apocynaceae. Ascomata 115-214 μ , asci 34-44 μ , spores 12 x 26-30 μ .

114. *Asterina diaphorella* Syd., Ann. Myc. 17:35. 1919. On *Sideroxylon*, Sapotaceae. Spores 26-30 x 11-14 μ . Differs from *A. laxiuscula* in its hemispheric, 6-7 μ hyphopodia. Syll. Fung. 24:471.

115. *Asterina saginata* Syd., Ann. Myc. 15:241. 1917. On *Polyalthia*, Anonaceae. Ascomata 200-300 μ , asci 45-50 μ , spores 27-30 x 12-14 μ . Syll. Fung. 24:443.

116. *Asterina xylosmae* Mendoza, Philipp. Jour. Sci. 49:185. 1932. On *Plectronia*, Rubiaceae. Ascomata 200-361 μ , asci 47-63 x 41-57 μ , spores 16-18 x 10-11 μ .

117. *Asterina plectroniae* Mendoza, Philipp. Jour. Sci. 49:186. 1932. On *Xylosma*, Flacourtiaceae. Ascomata 250-291 μ , asci 60-63 x 44-60 μ , spores 27-30 x 12-16 μ .

118. *Asterina drypetis* Ryan, Mycologia 16:180. 1924. On *Drypetes*, Euphorbiaceae. Ascomata 127-426 μ , asci 29-36 x 38-43 μ , spores 10-12 x 28-31 μ . Near *A. dispar*.

119. *Asterina fawcetti* Ryan, Mycologia 16:180. 1924. On *Eugenia*, Myrtaceae. Ascomata 190-264 μ , asci 24-48 x 51-65 μ , spores 9-12 x 29-31 μ .

120. *Asterina hippocrateae* Ryan, Mycologia 16:181. 1924. On *Hippocratea*, Hippocrataceae. Ascomata 96-104 μ , asci 36-45 x 26-38 μ , spores 31 x 14 μ .

121. *Asterina porriginosa* Syd., Leaflet Philipp. Bot. 5:1541. 1912. On *Ilex*, Aquifoliaceae. Ascomata 160-220 μ , asci 40-54 x 30-45 μ , spores 22-32 x 11-16 μ . Syll. Fung. 24:444; Abh. K. K. Zool.-Bot. Ges. 7:119. 1913. Theissen's key 117.

122. *Asterina ciferriana* Petr., Ann. Myc. 30:155. 1932. On *Caesalpinia*, Leguminosae. Ascomata 100-250 μ , asci 50-68 x 30-45 μ , spores 24-32 x 12-16 μ .

123. *Asterina sphaerotheca* Karst. and Roum., Rev. Myc. 12:76. 1890. On *Vitex*, Verbenaceae; *Mallea*, *Melia*, *Meliaceae*. Ascomata 80-100 μ , asci 40-50 or 40 x 60 μ , spores 24-32 x 13-16 μ . *Var. prodige* Theiss., Abh. K. K. Zool. Bot. Ges. 7:59. 1913. Syll. Fung. 24:475. 1926. Ascomata 110-180 or 250 x 140 μ , asci 50-65 x 40-48 μ , spores 30-36 x 13-16 μ . Syll. Fung. 9:383. Theissen's key 24.

124. *Asterina juruana* (Henn.) Theiss., Abh. K. K. Zool.-Bot. Ges. 7:84. 1913. *Seynesia juruana* Henn., Hedw. 43:376. 1904. Syll. Fung. 17:865. 1905. *Maublancia juruana* Arn., Ann. École Nat. Agr. Montp. 16:159. 1918. Syll. Fung. 17:865. 1905. On Casearia, Flacourtiaceae. Ascomata 500-650 μ , asci 140-190 x 25-30 μ , spores 28-32 x 9-12 μ . Estacion Agronomica de Moca, series B, no. 14, p. 70. Theissen's key 59.

125. *Asterina platasca* B. and C., Cuban Fungi no. 732, Jour. Linn. Soc. 10:373. 1869. On Passiflora, Passifloraceae. Ascomata 160-240 μ , asci 52-68 x 40-55 μ , spores 28-32 x 12-16 μ . Near *A. azarae* and possibly *A. arnaudia*. Syll. Fung. 1:40; Abh. K. K. Zool.-Bot. Ges. 7:85. 1913. Theissen's key 60.

126. *Asterina crotonicola* Pat. (not Doidge), Bull. Soc. Myc. Fr. 8:127. 1892. On Croton, Euphorbiaceae. Ascomata 130-160 μ , spores 32 x 15 μ . Syll. Fung. 9:256; Abh. K. K. Zool.-Bot. Ges. 7:110. 1913; Ann. Myc. 25-54. 1927. "Die Art wäre auf Identität mit *Asterina dispar* nachzuprüfen." Theissen's key 89.

127. *Asterina jahnii* Syd., Ann. Myc. 28:137. 1930. On Anonaceae. Ascomata 150-200 μ , asci 42-50 x 38-45 μ , spores 24-33 x 12-16 μ .

128. *Asterina psidii* Ryan, Mycologia 16:185. 1924. On Psidium, Myrtaceae. Ascomata 228 or 190 x 302 μ , asci 33-38 x 60-65 μ , spores 26-33 x 12-17 μ .

129. *Asterina paraguayensis* Speg., Fungi Guar. I, Anal. Soc. Ci. Argentina, 22:300. 1886; *ibid.* 26:51. 1888. *Seynesia paraguayensis* Speg., Syll. Fung. 9:1066. 1891. On Sapotaceae; Bignoniaceae; Lauraceae. Ascomata 160-200 μ , asci 40-45 or 50-70 x 35-40 μ , spores 28-33 x 12-15 μ . Abh. K. K. Zool.-Bot. Ges. 7:58. 1913; Öst. Bot. Zeitschr. 62:435. 1912. Theissen's key 23.

130. *Asterina camelliae* Syd. and Butl., Ann. Myc. 9:389. 1911. On Camellia, Theaceae; Miconia, Melastomataceae. Ascomata 200-300 μ , asci 70-100 x 25-35 μ , spores 30-33 x 16 μ . Syll. Fung. 24:474. 1926; Mycologia 16:183. 1925. Abh. K. K. Zool.-Bot. Ges. 7:83. 1913. Theissen's key 58.

131. *Asterina arnaudia* Ryan, Mycologia 16:184. 1925. On Passiflora, Passifloraceae. Ascomata 132-156 μ , asci 38-41 x 43-60 μ , spores 26-34 x 9-12 μ .

132. *Asterina chrysophylli* Henn., Hedw. 48:12. 1908. *Asterina valida* (Speg.) Sacc. and Trott., Syll. Fung. 22:544. 1913; *ibid.* 24:471. 1926; Fung. Paul. Rev. Mus. La Plata tab. 15, p. 29. 1896. *Asterella valida* Speg., Abh. K. K. Zool.-Bot. Ges. 7:67. 1913. On Chrysophyllum, Sapotaceae; Miconia, Melastomataceae. Ascomata 200-250 μ , asci 50-60 x 45-50 μ , spores 28-34 x 12-15 μ . Ann. Myc. 16:183. 1918; 28:378. 1930. Theissen's key 32.

133. *Asterina lepiniana* Mont., Abh. K. K. Zool.-Bot. Ges. 7:73. 1913.

Asterina pelliculosa Berk., Syll. Fung. 1:46. 1882; Ant. Voy. Crypt. p. 137. On Pavetta, Rubiaceae; Jasmini, Oleaceae. Ascomata 240-300 μ , asci 70-80 x 50-70 μ , spores 28-34 x 12-16 μ . Theissen's key 41.

134. *Asterina brysonimae* (Henn.) Theiss., Abh. K. K. Zool.-Bot. Ges. 7:71. 1913. *Lembosia brysonimae* Henn., Hedw. 43:265. 1904. Syll. Fung. 17:898. *Asterina brysonimicola* Henn., Hedw. 44:65. 1905. Syll. Fung. 17:875. On Brysonima, Malpighiaceae. Ascomata 200-300 or 300-500 x 200-250 μ , asci 60-90 x 54-60 μ , spores 28-34 x 12-17 μ . Theissen's key 37.

135. *Asterina versipoda* Ryan, Mycologia 16:188. 1924. On unknown host. Ascomata 224 μ , asci 36-50 μ , spores 29-34 x 12 μ .

136. *Asterina uncinata* Doidge, Trans. Roy. Soc. So. Afr. 8:252. 1920. On Rhamnus, Rhamnaceae. Ascomata 200-280 μ , asci 42-50 x 40-45 μ , spores 30-34 x 16-20 μ .

137. *Asterina meliosmaticola* Petr. and Cif., Ann. Myc. 30:160. 1932. On Meliosma, Sabiaceae. Ascomata 100-200 μ , asci 50-60 x 40-50 μ , spores 27-35 x 13-16 μ .

138. *Asterina verae-crucis* Theiss., Ann. Myc. 12:300. 1914. On Litsaea, Lauraceae. Asci 66 x 54 μ , spores 30-35 x 15-17 μ . Syll. Fung. 24:456.

139. *Asterina nodulifera* Syd., Philipp. Jour. Sci. 11:180. 1914. On Angelsenia, Rosaceae. Ascomata 250-340 μ , asci 40-55 x 38-44 μ , spores 30-35 μ . Syll. Fung. 24:467.

140. *Asterina bakeri* Syd. Ann. Myc. 14:367. 1916. On Daemonorops, Palmae. Ascomata 300-350 μ , asci 50-70 x 30-40 μ , spores 26-36 x 12-14 μ . Syll. Fung. 24:465.

141. *Asterina aucubae* Henn., Engl. Bot. Jahrb. 31:379. 1902. Syll. Fung. 17:878. *Asterina aucubae* (Sacc.) Theiss., Abh. K. K. Zool.-Bot. Ges. 7:83. 1913. *Lembosia catevararia* Mont. var *aucubae* Sacc., Hedw. 37:208. 1898. Syll. Fung. 16:663. On Aucubae, Cornaceae. Ascomata 160-200 μ , asci 54-62 x 34-45 μ , spores 26-36 x 12-14 μ . Ann. Myc. 10:187. 1912. Theissen's key 57.

142. *Asterina genipae* Ryan, Mycologia 16:180. 1924. On Genipa, Rubiaceae. Ascomata 192 μ , asci 41-58 μ , spores 29-36 x 14-16 μ .

143. *Asterina tetrazygiae* Ryan, Mycologia 16:183. 1924. On Tetrazygia, Melastomataceae. Ascomata 168-280 μ , asci 48-50 x 60-65 μ , spores 31-36 x 17-19 μ .

144. *Asterina fallaciosa* Syd., Ann. Myc. 15:240. 1917. On Canarium, Burseraceae. Ascomata 220-320 μ , asci 50-60 x 40-50 μ , spores 32-36 x 17-19 μ . Syll. Fung. 24:445.

145. *Asterina cylindrophora* Syd., Ann. Myc. 15:240. 1917. On Scolopia, Flacourtiaceae. Ascomata 160-250 μ , spores 34-36 x 18-20 μ . Syll. Fung. 24:454.

146. *Asterina carbonacea* Cke., Grev. 8:96. 1880. On leaves. Ascomata 140-170 μ , asci 55-70 x 40-50 μ , spores 35-36 x 14-18 μ . Syll. Fung. 1:42. 1882.

Var. acanthopoda Theiss. *Asterina acanthopoda* Speg., Fungi Guar. 2:47, no. 128; Syll. Fung. 9:385. 1891; Abh. K. K. Zool.-Bot. Ges. 9:70. 1913. *Asterina aesculi* Desm., Syll. Fung. 1:47. 1882. *Asterina sapotacearum* Speg., Anal. Mus. Nac. Buenos Aires 23:82. 1912; Syll. Fung. 9:385. 1891. On Chrysophyllum, Sapotaceae; Aesculus, Hippocastanaceae.

Var. huallagensis Theiss., Abh. K. K. Zoo.-Bot. Ges. 7:69. 1913. *Lembosia huallagensis* Henn., Hedw. 43:383. 1904; Syll. Fung. 17:898; Abh. K. K. Zool.-Bot. Ges. 7:69. 1913. On Sapindaceae. *Asterina acanthopoda* Speg. var. *hyptides* Rehm, Hedw. 40:160. 1901. On Hyptis, Labiatae. Syll. Fung. 16:1141.

Var. anacardii Ryan, Mycologia 16:186. 1924. On Anacardium, Anacardiaceae. Theissen's key 35.

147. *Asterina memecyloniae* Ryan, Mem. Dept. Agr. India 15:105. 1927. On Memecylon, Melastomataceae. Ascomata 132 μ , asci 64 x 36 μ , spores 36 x 14 μ .

148. *Asterina dipholidis* Petr. and Cif., Ann. Myc. 28:378. 1930. On Dipholis, Sapotaceae. Ascomata 200-300 μ , asci 45-60 x 40-45 μ , spores 28-36 μ long.

149. *Asterina subinermis* Syd., Leaflet Philipp. Bot. 6:1927. 1913. On leaves. Ascomata 175-220 μ , asci 42-55 x 35-45 μ , spores 32-37 x 14-16 μ . Syll. Fung. 24:475.

150. *Asterina guarantica* Speg., Anal. Soc. Ci. Argentina 22. 1886; *ibid.* 26:52. 1888; Syll. Fung. 9:1064. 1891. (sub *Seynesia*) Anal. Mus. Nac. Hist. Nat. Buenos Aires 23:80. 1912. *Seynesia guarantica* Speg., Fungi Guar., Pug. I, no. 299, Anal. Soc. Ci. Argentina 22. 1886. *Asterina schmideliae* Gaill., Bull. Soc. Myc. Fr. 13:181. 1897. Syll. Fung. 14:694. *Seynesia submegas* Henn., Hedw. 43:375. 1904; Syll. Fung. 17:867. *Asterina paraphysata* Starb. (not Winter), Asco. I, Regn. Exped. III, p. 12, Ark. f. Bot. II, no. 5, 1904; Syll. Fung. 17:878. 1905. On Trichilia, Guarea, Meliaceae; Schmidelia, Sapindaceae; Styra, Styraceae. Ascomata 150-250 or 230 x 180 μ , asci 65-68 x 50-55 μ , spores 30-38 μ . Abh. K. K. Zool.-Bot. Ges. 7:82. 1913; Öst. Bot. Zeitschr. 62:435. 1912; Ann. Myc. 25:60. 1927; 27:51. 1929. Theissen's key 56. "Ich vermute, dass *A. guarantica* Speg. im Theissen'schen Sinne eine Sammelart darstellt, so dass seine Diagnose nicht lediglich nach der auf. *Trichilia* lebenden typischen Form entworfen wurde. Hierauf dürften wohl die erwähnten Abweichungen zurückzuführen zu sein."

151. *Asterina guianensis* Ryan, Mycologia 16:182. 1924. On Miconia and Tamonea, Melastomataceae. Ascomata 96-144 μ , asci 48 x 28 μ , spores 24-38 x 12-14 μ .

152. *Asterina drypeticola* Petr. and Cif., Ann. Myc. 30:157. 1932. On *Drypetis*, Euphorbiaceae. Ascomata 200-400 μ , asci 55-65 x 45-50 μ , spores 30-38 x 14-18 μ .
153. *Asterina anisopterae* Syd., Ann. Myc. 12:556. 1914. On *Anisoptera*, Dipterocarpaceae. Ascomata 250-500 x 200-300 μ or 200-300 μ , asci 60-70 x 45-55 μ , spores 32-38 x 18-22 μ . Syll. Fung. 24:450.
154. *Asterina polythryria* Doidge, Trans. Roy. Soc. So. Afr. 8:258. 1920. On *Osyridicarpus*, Santalaceae. Ascomata 150-170 μ , or 190-200 x 140 μ , asci 26-40 x 20-24 μ , spores 16-20 x 6-7 μ . Doidge's key 22.
155. *Asterina shoreana* Sacc., Notae Myc. 23:61 (Acad. Ven.-Trent. 1917). On *Parashorea*, Dipterocarpaceae. Ascomata 240 μ , asci 55-60 μ , spores 30-40 x 16 μ . Syll. Fung. 24:451. 1926.
156. *Asterina laxiuscula* Syd., Philipp. Jour. Sci. 8:256. 1913. On *Sideroxylon*, Sapotaceae. Ascomata 150-220 μ , asci 55-75 x 40-50 μ , spores 32-40 x 15-18 μ . Syll. Fung. 24:471.
157. *Asterina robusta* Doidge, Trans. Roy. Soc. So. Afr. 8:256. 1920. On *Pittosporum*, Pittosporaceae. Ascomata 300-400 μ , asci 65-75 x 45-55 μ , spores 35-40 x 18-20 μ . Doidge's key 17.
158. *Asterina spectabilis* Syd. Philipp. Jour. Sci. 21:140. 1922. On *Flacourtia*, Flacourtiaceae. Ascomata 200-300 μ , asci 50-80 x 40-50 μ , spores, 35-42 x 18-20 μ .
159. *Asterina platypoda* Syd., Ann. Myc. 15:241. 1917. On *Urophylum*, Rubiaceae. Ascomata 250-350 μ , asci 70-85 x 55-70 μ , spores 37-42 x 18-21 μ . Syll. Fung. 24:468.
160. *Asterina inaequalis* Mont., Ann. Sci. Nat., ser. 4, 5:340. 1856; Syll. Fung. 1:41. *Asterina licaniae* Cke., Grev. 12:85. 1883; Syll. Fung. 9:380. On *Licania*, Rosaceae; *Hirtella*, Melastomataceae; *Melpighiaceae*. Ascomata 250-300 μ , spores 36-40 x 20-26 μ . *Var. nodulosa* Theiss., Abh. K. K. Zool.-Bot. Ges. 7:55. 1913. *Asterina nodulosa* Speg., Bol. Acad. Nac. Ci. Cordoba 11:563. 1889; Syll. Fung. 9:385. On *Guatteria*, Anonaceae. *Asterina obtusispora* Speg., Fungi Puigg. no. 354, Bol. Acad. Nac. Ci. Cordoba 11:564. 1889. Syll. Fung. 9:388. On *Tabebuia*, Bignoniaceae. Mycologia 16:180. 1924; Ann. Myc. 27:52. 1929. Theissen's key 17.
161. *Asterina schroeteri* (Rehm) Theiss., Abh. K. K. Zool.-Bot. Ges. 7:54. 1913. *Seynesia schroeteri* Rehm, Hedw. 37:326, fig. 14. 1898; Syll. Fung. 16:639. On *Chrysobalanus*, Rosaceae. Ascomata 220-300 μ , asci 60-70 x 42-46 μ , spores 38-42 x 11-13 μ . *Var. licaniae* Theiss., Abh. K. K. Zool.-Bot. Ges. 7:54. 1913. *Seynesia licaniae* Rehm (not *Asterina licaniae* Cke.), Ann. Myc. 7:538. 1909. On *Licania*, Rosaceae. Öst. Bot. Zeitschr. 62:435. 1912; Ann. Myc. 28:380. 1930. Theissen's key 16.
162. *Asterina pluriporus* Ryan, Mem. Dept. Agr. India 15:104. 1917. On *Shorea*, Dipterocarpaceae. Ascomata 264-848 μ , asci 80-84 x 84-104 μ , spores 24 x 40-42 μ .

163. *Asterina camariensis* Syd., Ann. Myc. 12:556. 1914. On *Parashorea*, Dipterocarpaceae. Ascomata 350-450 μ , asci 68-80 x 40-60 μ , spores 38-43 x 20-26 μ . Syll. Fung. 24:451.

164. *Asterina neolitseae* Yates, Philipp. Jour. Sci. 13:374. 1918. On *Neolitsea*, Lauraceae. Ascomata 150-170 μ , asci 60 x 25-30 μ , spores 44-46 x 14-15 μ . Syll. Fung. 24:465.

165. *Asterina stricta* Wint., Hedw. 32:103. 1892; Syll. Fung. 11:256. *Asterina hemispherica* Gaill., Bull. Soc. Myc. Fr. 13:179. 1897; Syll. Fung. 14:697. Host unknown. Ascomata 200-300 μ , asci 70-75 x 65-70 μ , spores 42-48 x 24-20 μ . Abh. K. K. Zool.-Bot. Ges. 7:60. 1913. Theissen's key 25.

166. *Asterina phyllostegiae* Stev. and Ryan, Bernice P. Bishop Mus. Bul. 19:73. 1925. On *Phyllostegia*, Labiatae. Ascomata 48-99 μ , asci 10-12 x 21-32 μ .

167. *Asterina crustacea* (Ell. and Ev.) Sacc. and Trott., Syll. Fung. 22:539. 1913. *Asterella crustacea* Ell. and Ev., in Millspaugh, Publ. Field Columb. Mus. Bot. II, no. 1, p. 15, tab. 51. 1900. On *Psidium*, Myrtaceae. Ascomata 500 μ , asci 70-80 x 15-20 μ .

168. *Asterina reticulata* (Kalch. and Cke.) Doidge, Trans. Roy. Soc. So. Afr. 8:252. 1920. *Asterostomella reticulata* v. Höhn., Frag. zur. Myk. no. 493. *Asterina reticulata* Kalch. and Cke., Grev. 9:33. 1880; Syll. Fung. 1:40. 1882. On *Celastrus*, *Elaeodendron*, *Pleurostyliia*, *Putterlichia*, *Celastraceae*; *Olinia*, *Oliniaceae*. Ascomata 220-240 μ , asci 40-43 x 23.5-26 μ , spores 20-23.5 x 8-9 μ , hyphopodia alternate, 1-celled, lobed.

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169. *Asterina poliotheae* (Syd.) Stev., n. comb. *Anariste poliotheae* Syd., Ann. Myc. 25:76. 1927. On *Phoebe*, Lauraceae. Ascomata 60-100 μ , asci 33-40 x 22-25 μ , spores 7-10 x 6-7.5 μ .

170. *Asterina violae* Henn., Hedw. 41:63. 1902; Syll. Fung. 17:876. On *Viola*, Violaceae. Ascomata 70:100 μ , asci 25-30 x 20-25 μ , spores 12-14 x 5.5-6 μ . "Die Art ist nahre verwandt mit *A. aspidii* durch Hyphen, Sporen und Membran-Struktur abweichend." Abh. K. K. Zool.-Bot. Ges. 7:100. 1913. Theissen's key 77.

171. *Asterina radians* Ellis, Jour. Myc. 8:276. 1893. On *Capparis*, *Capparidaceae*. Ascomata 200 μ , asci 35 x 20 μ , spores 12-15 x 5-5.5 μ . Doubtful species. Syll. Fung. 11:255. Theissen's key 103.

172. *Asterina lactucina* Syd., Ann. Myc. 29:232. 1931. On *Lactuca*, *Compositae*. Ascomata 80-120 μ , asci 20-28 μ , spores 12-16 x 6-8 μ .

173. *Asterina advenula* Syd., Ann. Myc. 25:46. 1927. On *Rondeletia*, *Rubiaceae*. Ascomata 70-130 μ , asci 25-33 μ , spores 13-17 x 7-9.5 μ .

174. *Asterina pavoniae* Werd., Rep. Spec. Nov. regin. veg. 19:49. 1923. On *Pavonia*, *Malvaceae*. Ascomata 100 μ , asci 35-42 x 25-40 μ , spores 7.5-9 x 14-16 μ .

175. *Asterina leptalea* Syd., Ann. Myc. 29:233. 1913. On *Helicteris*, Sterculiaceae. Ascomata 90-150 μ , asci 25-33 μ , spores 13-17 x 7-9.5 μ . "Die dazu zugehörige *Asterostomella*-Nebenfruchtform hat etwas kleinere, meist nur ca. 45-100 μ grosse, sonst ganz übereinstimmend gebaute Gehäuse, in welchen sehr breit eiförmige, ellipsoidische oder fast kugelige durchscheinend schwarz-braune einzellige, 12-16 x 11-14 μ , grosse Konidien gebildet werden, die keine hellere Gurtelzone zeigen."

176. *Asterina* van der Bijli Werd., Rep. Spec. Nov. regni veg. 19:49. 1923. On *Heteropyxis*, Bombacaceae. Ascomata 160 μ , asci 30-35 x 26-28 μ , spores 15-17.5 x 5-8 μ . So. Afr. Jour. Sci. 25:182. 1928.

177. *Asterina phenaxis* Syd., Ann. Myc. 25:66. 1927. On *Phenax*, Urticaceae. Ascomata 60-125 μ , asci 35-40 x 25-30 μ , spores 15-18 x 7.5-10 μ .

178. *Asterina diplopoda* Syd., Ann. Myc. 25:56. 1927; 28:136. 1930. On *Solanum*, Solanaceae. Ascomata 70-125 μ , asci 33-40 x 25-32 μ , spores 16-18 x 7-8.5 μ . On *Solanum callicarpaefolium* the basal membrane is not distinct.

179. *Asterina tenuis* Wint., Hedw. 26:94. 1886. On *Claoxylon*, Dalachampia, Acalypha, Euphorbiaceae. Ascomata 85-130 μ , asci 70-75 x 26-32 μ , spores 16-18 x 8-9 μ . Dubious. Syll. Fung. 9:389. Theissen's key 106.

180. *Asterina concinna* Syd., Ann. Myc. 28:134. 1930. On *Macrocephis*, Asclepiadaceae. Ascomata 90-160 μ , asci 25-32 μ , spores 18.5-16 x 8-10 μ .

181. *Asterina celtidicola* Henn., Hedw. 44:64. 1905; Syll. Fung. 17:876; Abh. K. K. Zool.-Bot. Ges. 7:94. 1913. On *Celtis*, Ulmaceae. Ascomata 85-135 μ , asci 23-30 x 26-33 μ , spores 9-8 x 18-16 μ . *Var. microspora* Doidge, Trans. Roy. Soc. So. Afr. 8:160. 1920; *Bothalia* 2:204. 1927. On *Maeura*, Capparis, Capparidaceae; *Oncoba*, Kiggelaria, Flacourtiaceae. *Var. capparidis* Theiss., Abh. K. K. Zool.-Bot. Ges. 7:94. 1913; Ann. Myc. 26:439. 1928. *Asterina capparidis* Syd. and Butl., Ann. Myc. 9:390. 1911. "Var. *microspora* differs from the type and also from var. *capparidis* chiefly in the size of the spores and asci. Var. *capparidis* differs from the type in the short cubical cells composing the ascomata, which are not so delicate as those of the type." Theissen's key 69.

182. *Asterina consociata* Wint., in Speg., Fungi Guar. 2:149, no. 131. On *Maclura*, Moraceae. Ascomata 80-100 μ , asci 35-40 x 25-30 μ , spores 18 x 9 μ . *Var. rectangularis* Rehm, Hedw. 40:161. 1901. Syll. Fung. 16:1141. On Euphorbiaceae. Perhaps this variety is *A. diplocarpa* Cke. or *A. eupomatiae* var. *dalachampiae*. Theiss. Syll. Fung. 9:387; Abh. K. K. Zool.-Bot. Ges. 7:98. 1913. Theissen's key 74.

183. *Asterina isothea* Syd., Ann. Myc. 25:64. 1927. On *Triumfetta*, Tillaceae. Ascomata 100-160 μ , asci 32-36 x 27-33 μ , spores 14-19 x 7.5-9 μ . Coindia: *Asterostomella isothea* Syd.

184. *Asterina marginalis* Petr., Ann. Myc. 29:240. 1931. On *Claoxylon*, Euphorbiaceae. Ascomata 80-150 μ , asci 22-32 μ , spores 16-19 x 7-9 μ .

185. *Asterina congesta* Cke., Grev. 8:95. 1879. On *Santalum*, Santalaceae. Ascomata 100-150 μ , spores 20 x 10 μ . Near *A. megalospora* B. and C. and *A. azarae* Lév. Conidia: *Asterostomella*.

186. *Asterina aganosmae* Petr., Ann. Myc. 29:238. 1931. On *Aganosma*, Apocynaceae. Ascomata 100-160 μ , asci 28-36 μ , spores 16-19 x 7-9 μ .

187. *Asterina banisteriae* Syd., Ann. Myc. 27:50. 1929. On *Banisteria*, Malpighiaceae. Ascomata 80-160 μ , asci 25-35 μ , spores 15-20 x 7-9 μ .

188. *Asterina tetracerae* Syd., Ann. Myc. 29:235. 1931. On *Tetracera*, Dilliniaceae. Ascomata 80-160 μ , asci 25-35 μ , spores 15-20 x 7-9 μ .

189. *Asterina tertia* Rac., ap. Theiss., Abh. K. K. Zool.-Bot. Ges. 7:103. 1913. On *Adhatoda*, *Crosandra*, *Ruellia*, Acanthaceae. Ascomata 120-160 μ , asci 40-48 x 20-23 μ , spores 16-20 x 8-10 μ . Sub *Asterina adhatodae* Koord. "Verwandt mit *A. lawsoniae* doch sind die Konidienwands gleichmassig dick und gleichmassig braun, ohne den hellen aequatorialen Ring." *Var. africana* Doidge, Trans. Roy. Soc. So. Afr. 8:264. 1920. On *Hypoestes*, *Isoglossa*, *Dicliptera*, *Peristrophe*, Acanthaceae. Ascomata and spores smaller than the type. Syll. Fung. 24:443; Jour. Dept. Agr. Puerto Rico 13:231. 1929. Theissen's key 81.

190. *Asterina cupheae* Syd., Ann. Myc. 25:55. 1927. On *Cuphea*, Lythraceae. Ascomata 120-180 μ , asci 32-40 x 25-32 μ , spores 17-20 x 7-9 μ .

191. *Asterina jacaratiae* Theiss., Ann. Myc. 14:269. 1916. On *Jacaratia*, Caricaceae. Ascomata 100-140 μ , asci 54 x 32 μ , spores 17-20 x 9-10 μ . Conidia: *Asterostomella jacaratiae* Theiss. Syll. Fung. 24:446.

192. *Asterina clausenicola* Doidge, Trans. Roy. Soc. So. Afr. 8:263. 1920. On *Clausena*, Rutaceae. Ascomata 110-140 μ , asci 27-30 x 23-24 μ , spores 19-20 x 6.4-8 μ . Doidge's key 28.

193. *Asterina acalyphae* Syd., Ann. Myc. 23:395. 1925. On *Alcalypha*, Euphorbiaceae. Ascomata 100-180 μ , asci 27-45 x 24-32 μ , spores 17-21 x 10-12 μ . Conidia: *Asterostomella acalyphae*.

194. *Asterina wrightiae* Syd., Ann. Myc. 29:236. 1931. On *Wrightia*, Apocynaceae. Ascomata 100-180 μ , asci 30-40 x 22-28 μ , spores 18 x 21 x 8-10.5 μ .

195. *Asterina amadelpha* Syd., Ann. Myc. 27:56. 1929. On *Conostegia*, Melastomataceae. Ascomata 80-170 μ , asci 32-40 x 20-25 μ , rarely 55 μ , spores 17-22 μ . "Die Art gehört in die Verwandtschaft von *A. melastomataceae* (Henn.) Theiss., und *A. transiens* Theiss., erscheint aber von beiden genügend verschieden."

196. *Asterina diplocarpa* Cke., Grev. 10:129. 1882; Syll. Fung. 9:381.

Asterina similis Cke., Grev. 10:130. 1881. *Asterina sidae* Earle, Plants of Puerto Rico 6333, Bull. N. Y. Bot. Gard. 3:310. 1900. *Asterina kwangensis* Henn., in herb. Berlin. *Asterina huallagensis* Henn. (not Theiss.), Hedw. 43:372. 1904; Syll. Fung. 17:879. *Asterina sidicola* Ryan, Mycologia 16:181. 1924. On *Corchorus*, Tiliaceae; *Croton*, Euphorbiaceae; *Sida*, *Abutilon*, Malvaceae; *Asclepiadaceae*. Ascomata 85-135 μ , asci 28-42 x 24-30 μ , spores 17-22 x 8-10 μ . *Var. cesticola* Ryan, Mycologia 16:187. 1924. On *Cestrum*, Solanaceae. Ascomata 132-168 μ , asci 31 x 36 or 24 μ in diameter, spores 19 x 7 μ . Syll. Fung. 22:538; Abh. K. K. Zool.-Bot. Ges. 7:106. 1913; N. Y. Acad. Sci. 8:19. 1926; Ann. Myc. 28:135. 1930; Mycologia 17:132. 1925. Theissen's key 84.

197. *Asterina aemula* Syd., Ann. Myc. 25:48. 1927. On Lauraceae. Ascomata 120-200 μ , asci 35-45 x 25-33 μ , spores 17-22 x 8-10 μ . "Die Art steht zweifellos der *A. ampullulipeda* Speg. and *A. hamata* Syd. sehr nahe."

198. *Asterina travancorensis* Syd., Ann. Myc. 13:38. 1915. On *Marsdenia*, *Asclepiadaceae*. Ascomata 130-160 μ , asci 26-35 x 22-28 μ , spores 18-22 x 9-11 μ . Syll. Fung. 24:444.

199. *Asterina oligopoda* Syd., Ann. Myc. 28:139. 1930. On *Gonzalea*, *Rubiaceae*. Ascomata 100-170 μ , asci 36-42 x 23-30 μ , spores 17-23 x 7.5-10 μ .

200. *Asterina dorsteniae* Syd., Ann. Myc. 25:27. 1927. On *Dorstenia*, *Moraceae*. Ascomata 100-150 μ , asci 33-45 x 25-28 μ , spores 17-23 x 10-12 μ . "Über die dazugehörige Konidiengeneration vgl. *Asterostomella dorsteniae* Syd."

201. *Asterina benguetensis* Petr., Ann. Myc. 29:239. 1936. On *Solanum*, *Solanaceae*. Ascomata 100-200 μ , asci 28-36 μ , spores 17-23 x 9-12 μ .

202. *Asterina hamata* Syd., Ann. Myc. 25:61. 1927. On *Phoebe*, *Lauraceae*. Ascomata 100-150 μ , asci 32-55 x 25-35 μ , spores 20-23 μ . "Die Art steht zweifellos der *A. ampullulipeda* Speg. nahe, unterscheidet sich aber nach der von Theissen (Die Gattung *Asterina* p. 68) gegebenen Beschreibung und Abbildung dieser Art namentlich durch das ganz unregelmässig netzartig verzweigte Mysel mit oft gegenständigen, fast stets mehr weniger stark gekrümmten Hyphopodien."

203. *Asterina solanicola* B. and C., Cuban Fungi 738, Jour. Linn. Soc. 10:374. 1868. *Asterina hyphaster* Henn., Hedw. 41:299. 1902; Syll. Fung. 17:876. 1905. *Asterina turnerae* Henn., Hedw. 44:371. 1904. Syll. Fung. 17:878. *Dimerosporium hyphaster* Arn., Ann. Fcole Nat. Agr. Montp. 16:180. 1918. On *Cestrum*, *Solanum*, *Solanaceae*; *Malvastrum*, *Pavonia*, *Malvaceae*; *Casearia*, *Flacourtiaceae*; *Turnera*, *Turneraceae*; *Croton*, *Euphorbiaceae*; *Clusia*, *Guttiferaceae*; *Asclepiadaceae*.

Ascomata 80-140 μ , asci 25-32 μ in diameter or 40 x 34 μ , spores 17-24 x 8-12 μ .

Var. cristata Theiss., Abh. K. K. Zool.-Bot. Ges. 7:105. 1913. *Asterina cristata* Speg., Fungi Guar. 2:26; Syll. Fung. 9:391. 1891. *Asterina triloba* Earle, Bull. N. Y. Bot. Gard. 3:310. 1905. *Asterina balansae* var. *ildefonsiae* Rehm, Ann. Myc. 10:24. 1912. Syll. Fung. 22:542; Abh. K. K. Zool.-Bot. Ges. 7:104. 1913; Mycologia 17:134. 1925. Theissen's key 83.

204. *Asterina phoebes* Syd., Ann. Myc. 25:68. 1927. On Nectandra, Phoebe, Lauraceae. Ascomata 130-200 μ , asci 30-40 x 22-35 μ , spores 18-24 x 7.5-9 μ . Ann. Myc. 27:52. 1929.

205. *Asterina azarae* Lév., Ann. Sci. Nat. 3:59. 1845; Syll. Fung. 1:51. *Asterula azarae* Sacc., Syll. Fung. 9:377. 1891. *Asterina darwini* Berk., Fl. Antarct. 2:452, tab. 16, fig. 2. *Dimerosporium azarae* Arn., Ann. École Nat. Agr. Montp. 16:177. 1918. On Azara, Flacourtiaceae. Ascomata 200-350 x 100-200 μ , asci 40 x 35-38 μ , spores 20-24 x 8-10 μ . Conidia: Asterostomella. Syll. Fung. 9:393; Abh. K. K. Zool.-Bot. Ges. 7:101. 1913; Ann. Myc. 25:52. 1927; 10:9. 1912.

206. *Asterina loranthicola* Syd., Ann. Myc. 12:266. 1914. On Loranthus, Loranthaceae. Ascomata 100-160 μ , asci 30-38 x 24-30 μ , spores 20-24 x 8-11 μ . Syll. Fung. 24:457.

207. *Asterina sodalis* Syd., Ann. Myc. 26:95. 1928. On Symplocus, Symplocaceae. Ascomata 120-150 μ , asci 40-50 x 36-36 μ , spores 22-24 x 10-12 μ .

208. *Asterina malaisiae* Syd., Ann. Myc. 29:228. 1931. On Malaisia, Moraceae. Ascomata 90-130 μ , asci 30-36 μ , spores 18-25 x 9-11 μ .

209. *Asterina chloranthi* Syd., Ann. Myc. 29:227. 1931. On Chloranthus, Chloranthaceae. Ascomata 90-160 μ , asci 30-40 x 27-34 μ , spores 18-25 x 8-11 μ .

210. *Asterina bataaensis* Petr., Ann. Myc. 29:229. 1931. On Phaleria, Thymelaceae. Ascomata 90-150 μ , asci 30-40 x 25-33 μ , spores 19-25 x 9-12 μ .

211. *Asterina solanicoloides* Rehm, Hedw. 36:150. 1896. *Asterina vagans* var. *solanicoloides* Rehm, Abh. K. K. Zool.-Bot. Ges. 7:95. 1913. On Solanum, Solanaceae. Ascomata 100-170 μ , asci 50-60 x 30-40 μ , spores 20-25 x 9-12 μ . Abh. K. K. Zool.-Bot. Ges. 7:97. 1913. Theissen's key 73.

212. *Asterina consobrina* Syd., Ann. Myc. 25:49. 1927. On Solanum, Solanaceae. Ascomata 60-150 μ , asci 40-50 x 30-38 μ , spores 20-25 x 11-13 μ . "Unter den zahlreichen Solanum-gewohnenden Arten der Gattung kommt für die vorliegende Form nur *A. solanicola* B. and C. et Betracht. Von dieser Art unterscheidet sich die neue Art besonders durch die meist nicht oder nur wenig gelappten Hyphopodien und die durch schnittlich

etwas grosseren, mit glattem Epispor versehenen Sporen. Auch gehört nach Theissen *A. solanicola* zu den Arten der Gattung, die eine deutlich ausgebildete Basalmembran besitzen. Dies ist bei der neuen Form aber nicht der Fall."

213. *Asterina caricarum* Rehm, Hedw. 35:161. 1895. Syll. Fung. 14:695; Ann. Myc. 31:144. 1933. *Asterostomella caricae* Henn., Hedw. 44:391. 1904. *Seynesia balansae* Speg., in Ule col. no. 1134 and 970, herb. Berlin. On *Carica*, *Caricaceae*. Ascomata 100-140 μ , asci 42-48 or 50 x 28 μ , spores 22-25 x 10-12 μ . *Var. microspora* Theiss., Abh. K. K. Zool.-Bot. Ges. 7:95. 1913. Spores 17-22 x 8-11 μ . Theissen's key 71.

214. *Asterina venezuelana* Syd., Ann. Myc. 28:144. 1930. On *Cliedemia*, *Melastomataceae*. Ascomata 180-250 μ , asci 48-60 x 24-30 μ , spores 20-26 x 11-13 μ .

215. *Asterina escharoides* Syd., Abh. K. K. Zool.-Bot. Ges. 7:101. 1913. On *Platea*, *Icacinaeae*; *Pittosporium*, *Pittosporaceae*; *Quisqualis*, *Combretaceae*. Ascomata 130-175 μ , asci 26-40 x 24-32 μ , spores 17-22 x 8-12 μ . Syll. Fung. 24:447, 455; Philipp. Jour. Sci. 8:489. 1914; Leaflet Philipp. Jour. Sci. 4:1155. 1911. Theissen's key 86.

216. *Asterina megalospora* B. and C., Jour. Linn. Soc. 10:373. 1869. *Asterina passifloricola* Ryan, Mycologia 16:183. 1924. *Asterina cubensis* Sacc. and Syd., Syll. Fung. 14:698. 1899. On *Passiflora*, *Passifloraceae*. Ascomata 120-200 or 200-240 x 120-140 μ , asci 45-50 x 35-40 μ , spores 21-26 x 10-11 μ . Conidia: *Asterostomella*. *Var. meizopoda* Theiss., Abh. K. K. Zool.-Bot. Ges. 7:107. 1913. *Asterina passiflorae* Sacc., Syll. Fung. 17:877. 1905. *Asterella passiflorae* Henn., Syll. Fung. 1:41. 1882. Ascomata 120-180 μ , asci 30-40 x 20-25 μ , spores 16-22 x 8-12 μ . Ann. Myc. 28:138. 1930; 25:66. 1927. Theissen's key 85.

217. *Asterina denigrata* Pat., Ann. Myc. 27:57. 1927. On *Blakea*, *Melastomataceae*. Ascomata 30-130 μ , asci 42-50 x 38-40 μ , spores 22-26 x 10-11 μ .

218. *Asterina vagans* Speg., Fungi Guar. II, no. 127. 1883. *Dimerosporium vagans* Arn., Ann. École Nat. Agr. Montp. 16:176. 1918. On *Solanum*, *Solanaceae*; *Tournefortia*, *Cordia*, *Borraginaceae*. Ascomata 100-150 μ , asci 40-50 x 25-30 μ , spores 22-26 x 10-12 μ . Syll. Fung. 9:390. *Var. subreticulata* Theiss., Abh. K. K. Zool.-Bot. Ges. 7:95. 1913. *Asterina subreticulata* Speg., Fungi Guar. I, no. 138; Syll. Fung. 9:390. 1891. *Myxasterina subreticulata* v. Höhn., Frag. zur Myk. no. 422. On *Solanum*, *Cestrum*, *Solanaceae*; *Rinorea*, *Violaceae*. Abh. K. K. Zool.-Bot. Ges. 7:96. 1913; Trans. Roy. Soc. So. Afr. 8:261. 1920; Mycologia 16:180. 1924; Ann. Myc. 25:76. 1927; 27:54. 1929; 28:144. 1930. Theissen's key 70.

219. *Asterina coriacea* Speg., Bol. Acad. Nac. Ci. Cordoba, 11:560. 1889. On *Cestrum*, *Solanaceae*. Ascomata 100-180 or 150-300 x 90-150 μ ,

asci 44-56 x 32-36 μ , spores 22-26 x 10-12 μ . Syll. Fung. 9:390; Mycologia 17:133. 1925; Abh. K. K. Zool.-Bot. Ges. 7:108. 1913; Ann. Myc. 31:144. 1933. Theissen's key 87.

220. *Asterina indecora* Syd., Ann. Myc. 25:63. 1927. On *Malpighia*, Malpighiaceae. Ascomata 90-140 μ , asci 33-45 x 25-37 μ , spores 22-26 x 11-13 μ . "Die Schlauchform ist nur sehr spärlich entwickelt, meist wird nur die dazu gehörige *Asterostomella indecora* angetroffen."

221. *Asterina pseudopelliculosa* Speg., Fungi Puigg. no. 356, Bol. Acad. Nac. Ci. Cordoba 11:566. 1889. On *Ipomea*, Convolvulaceae. Ascomata 80-120 μ , asci 40-55 x 30-35 μ , spores 18 x 8 μ . Syll. Fung. 9:391. 1891. *Var. peraffinis* (Speg.) Theiss., Abh. K. K. Zool.-Bot. Ges. 7:104. 1913. *Asterina peraffinis* Speg., Fungi Puigg. no. 355, Bol. Acad. Nac. Ci. Cordoba 11:565. 1889. Syll. Fung. 9:392. 1891. On *Tylophora*, Asclepiadaceae. *Form africana*: *Asterina strophanthi* Henn., Engl. Jahrb. 38:125. 1905. Abh. K. K. Zool.-Bot. Ges. 7:104. 1913. On *Strophanthus*, Apocynaceae; *Ipomea*, Convolvulaceae. Ascomata 70-120 μ , asci 25-38 x 18-22 μ , spores 13-16 x 7-8 μ . Syll. Fung. 22:541. Theissen's key 82.

222. *Asterina aphanes* Petr., Ann. Myc. 27:49. 1929. On *Rapanea*, Myrsinaceae. Ascomata 250-450 μ , asci 45-55 x 25-35 μ , spores 21-27 x 9-12 μ .

223. *Asterina mexicana* Ell. and Ev., Bull. Torr. Bot. Club 26:51, 1900. On *Agave*, Amaryllidaceae. Ascomata 110-150 μ , asci 40-60 x 20-30 μ , spores 22-27 x 8-10 μ . Doubtful species. Syll. Fung. 16:648. 1902; Abh. K. K. Zool.-Bot. Ges. 7:112. 1913. Theissen's key 97.

224. *Asterina schlechteriana* Syd., Ann. Myc. 25:71. 1927; *ibid.* 27:54. 1929. On *Clidemia*, Melastomataceae. Ascomata 170-280 μ , asci 55-65 x 30-40 μ , spores 22-32 μ .

225. *Asterina erebia* Syd., Ann. Myc. 25:59. 1927; *ibid.* 27:51. 1929. On *Palicourea*, Rubiaceae. Ascomata 150-300 μ , asci 55-65 μ , spores 26-32 x 13-16 μ .

226. *Asterina orthosticha* Syd., Ann. Myc. 28:140. 1930. On *Dolioscarpi*, Dilleniaceae. Ascomata 150-200 μ , asci 50-58 x 45-52 μ , spores 30-35 μ . Conidia: *Asterostomella orthosticha*.

227. *Asterina pulchella* Petr., Ann. Myc. 27:53. 1929; *ibid.* 28:142. 1930. On *Securidaca*, Polygalaceae. Ascomata 180-350 μ , asci 42-70 x 35-45 μ , spores 24-35 x 13-15 μ .

228. *Asterina clemensiae* Petr., Ann. Myc. 29:231. 1931. On *Polyalthia*, Anonaceae. Ascomata 70-180 μ , asci 45-50 μ , spores 28-35 μ .

229. *Asterina styracina* Syd., Ann. Myc. 25:73. 1927. On *Styrax*, Styracaceae. Ascomata 150-250 μ , asci 50-60 μ , spores 27-36 x 16-20 μ . "*A. styracis* Theiss. und *A. guaranitica* Speg. sind zunächst vollständig von der vorliegenden Art verschieden. *A. multiplex* Rehm welche von Theissen wohl zu Unrecht mit *A. brachystoma* (Rehm) Theiss. vereinigt wurde, unterscheidet sich von meinen Exemplaren durch anderen Kontext

der Thyriothecien und Auftreten deutlicher Paraphysen. Die vierte entsprechen doch wurde auch nach der Beschreibung von Theissen etwas anders gebaute Thyriothecien und vor allen Dingen deutlich ungleich septierte Sporen besitzen."

230. *Asterina buttneriae* Theiss., Abh. K. K. Zool.-Bot. Ges. 7:99, tab. 2, fig. 19-21; tab. 4, fig. 15. 1913. On *Buttneria*, Sterculiaceae. Ascomata 140-170 μ , asci 35-48 x 30-35 μ , spores 23-27 x 9-11 μ . Syll. Fung. 24:473. Theissen's key 76

231. *Asterina radio-fissilis* (Sacc.) Theiss., Frag. brasil. no. 115, Ann. Myc. 10:22. 1912. *Dimerium radio-fissile* Sacc., F. aliquot afr., Bol. Soc. Broteriana 21:21. 1904. On *Kraussia*, Rubiaceae. Ascomata 80-140 μ , asci 32-42 x 25-30 μ , spores 17-19 x 8-10 μ . *Var. macrospora* Theiss., Abh. K. K. Zool.-Bot. Ges. 7:97. 1913. Spores 25-28 x 11-13 μ . Theissen's key 72.

232. *Asterina papillata* Syd., Ann. Myc., 14:92. 1916. On *Capparis*, Capparidaceae. Ascomata 140-200 μ , asci 38-48 x 35-42 μ , spores 24-28 x 12-13 μ . Syll. Fung. 24:446.

233. *Asterina tacsoniae* Pat., Bull. Soc. Myc. Fr. 40:147. 1893; Syll. Fung. 11:255. *Scynesia lagerheimii* Rehm, Hedw. 37:325. 1898; Syll. Fung. 16:640. On *Tacsonia*, Passifloraceae. Ascomata 100-180 μ or 150-300 x 90-150 μ , asci 50-60 x 35 μ , spores 22-29 x 10-13 μ . *Var. passiflorae* Ryan, Mycologia 16:184. 1924; N. Y. Acad. Sci. 8:20. 1926. On *Passiflora*, Passifloraceae. Ascomata 132-156 μ , asci 24 x 29-32 μ , spores 14-19 x 6-7 μ . Theissen's key 79.

234. *Asterina sponiae* Rac., Parasit. Algen und Pilze Javas 3:34. 1900; Syll. Fung. 16:647. 1902. *Asteronella epitrema* Cke., Grev., 20:7. 1891. *Asterina stylospora* Cke., Grev. 10:129. 1881. On *Sponia*, Trema, Ulmaceae. Ascomata 100-120 μ , asci 50-65 x 42-52 μ , spores 25-30 x 12-16 μ . Abh. K. K. Zool.-Bot. Ges. 7:100. 1913; Ann. Myc. 25:92. 1927; *ibid.* 21:103. 1923; *ibid.* 28:143. 1930; *ibid.* 29:225. 1931. Theissen's key 78.

235. *Asterina pittieri* Bomm. and Rouss., Bull. Soc. Roy. Bot. Belg., p. 156. 1896. On *Angelica*, Umbelliferae. Ascomata 126-150 μ , asci 32-47 μ , spores 28-36 x 18-28 μ . Syll. Fung. 14:695. Theissen says (86) that this is a doubtful species.

236. *Asterina ramonensis* Syd., Ann. Myc. 25:29. 1927. Host not known. Ascomata 180-250 μ , asci 60-75 x 50-60 μ , spores 33-39 μ . "Die Art steht der *A. paraguayensis* Speg. nahe, ist aber zweifellos gut verschieden."

It seems advisable to keep the following species in the genus *Asterina*, even though they have somewhat elongated ascomata. The description of the genus *Asterina* reads, "ascomata circular," but in the general description for *Dimerosporium* Fckl. we read, "ascomata subglobose." Further, the type species, *A. azarae* Lév., has subglobose ascomata.

Subgenus DIMEROSPORIUM Theissen

237. *Asterina psychotriae* Ryan, Mycologia 16:185. 1924. On *Psychotria*, Rubiaceae. Ascomata 94-240 x 84-201 μ , asci 24-48 μ , spores 14-19 x 7-12 μ .

238. *Asterina sphaerelloides* Speg., Fungi Guar. non nulli, no. 123; Rev. Argentina Hist. Nat. I, Buenos Aires, 1891; Syll. Fung. 11:255. 1895. *Asterina ellisii* Sacc. and Syd., Syll. Fung. 14:693. 1899. *Asterina loranthacearum* Rehm, Ann. Myc. 5:522. 1907; Abh. K. K. Zool.-Bot. Ges. 7:78. 1913. On *Ilex*, Aquifoliaceae; *Clematis*, Ranunculaceae. Ascomata 70-120 x 100-130 μ , asci 30-35 x 25-30 μ , spores 20-24 x 10-12 μ . Syll. Fung. 22:541; Sitz. K. Akad. Wiss. Wien 129:140. 1920.

239. *Asterina elaeagni* (Syd.) Syd., Ann. Myc. 29:225. 1931. *Asterinella elaeagni* Syd., Ann. Myc. 18:101. 1920. On *Elaeagnus*, Elaeagnaceae. Ascomata 90-160 x 70-100 μ , asci 25-35 x 25-30 μ , spores 18-20 x 7-8 μ . Syll. Fung. 24:481.

240. *Asterina casjerae* Ryan, Mem. Dept. Agr. India 15:103. 1927. On *Casjera*, Opiliaceae. Ascomata 160-200 x 120-144 μ , asci 28-32 x 36-44 μ , spores 18-22 x 8 μ .

241. *Asterina salaciae* Allesch., Hedw. 36:235. 1897; Syll. Fung. 14:694. *Dimerosporium salaciae* Henn., Hedw. 35:105. 1896; Syll. Fung. 14:694; Abh. K. K. Zool.-Bot. Ges. 7:80. 1913. On *Salacia*, Hippocrataceae. Ascomata 280 x 150-180 μ , asci 40-32 or 54 x 35 μ , spores 22-25 x 10-11 μ .

242. *Asterina subglobulifera* v. Höhn., Sitz. K. Acad. Wiss. Wien 129:141. 1920. On *Palmae*. Ascomata 500 x 300 μ , asci 68-74 x 52-54 μ , spores 40-44 x 18-20 μ . Theissen's key 19.

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243. *Asterina costaricensis* Syd., Ann. Myc. 25:56. 1927. On *Jacobinia*, Acanthaceae. Ascomata 170 x 150 μ , asci 24-33 x 20-27 μ , spores 15-18 x 7-9 μ .

244. *Asterina azarae* Lév. See No. 205.

38. ASTEROMYXA Theissen and Sydow

Annales Mycologici 15:419. 1917.

Type: *A. hirtula* (Speg.) Theiss. and Syd.

Characters: Mycelium present, no hyphopodia; ascomata radiate, ostiolate, spiny, slimy-dissolvent, aparaphysate, spores brown, 2-celled.

1. *Asteromyxa hirtula* (Speg.) Theiss. and Syd., l. c. *Dimeriella hirtula* Speg. On *Baccharis*, Compositae. Ascomata 60-90 μ , asci 35-40 x 15-18 μ , spores 14 x 5 μ . Syll. Fung. 22:37. 1913.

2. *Asteromyxa surigaoensis* Mendoza, Philipp. Jour. Sci. 49:190. 1932. On Anonaceae. Ascomata 86-102 μ , asci 31-44 x 19-27 μ , spores 14-19 x 8-9 μ .

3. *Asteromyxa inconspicua* Doidge, Bothalia 2:199. 1927. On Chilianthus, Loganiaceae. Ascomata 160-270 μ , asci 30-35 x 22-24 μ , spores 17-22 x 6-8.5 μ .

39. THALLOCHAETE Theissen

Annales Mycologici 11:501. 1913.

Type: *T. ingae* Theiss.

Characters: Ascomata superficial, inverse, radiate; mycelium branching, septate, producing erect setae; asci 8-spored, paraphysate; spores brown, 2-celled; conidia 4-celled, no hyphopodia.

1. *Thallochaete ingae* Theiss., l. c., fig. 4; tab. 21, fig. 6. On Inga, Leguminosae. Ascomata 100-180 μ , asci 28-35 x 16-20 μ , spores 18-22 x 6-8 μ .

40. ASTERINELLA Theissen

Annales Mycologici 10:160. 1912.

Type: *A. puiggarii* (Speg.) Theiss.

Characters: Mycelium present, non-hyphopodiate; ascomata dimidiate, radiate, ostiolate; asci paraphysate; spores brown, 2-celled.

Literature: Ann. Myc. 10:101. 1912.

Synonymous genera:

1) *Hariotula* Arn., Ann. École Nat. Agr. Montp. 16:201. 1918. Type: *H. loranthi* (K. and H.) Arn. This is considered as *Asterinella*.

2) *Opeasterinella* Speg., Bol. Acad. Nac. Ci. Cordoba 23:498. 1919. Type: *O. brasiliensis* Speg., Fung. al Paul. n. 79, l. c. This genus does not seem to be distinct from *Asterinella*. *Asterinella* formerly contained both paraphysate and aparaphysate forms. The aparaphysate species have been removed and placed in the genus *Prillieuxina* Arn. The species are arranged in order of maximum spore length.

1. *Asterinella cupressina* (Rehm) Theiss., Broteria 10:110. 1912. *Asterina cupressina* Cke., Grev. 6:17. 1877; Syll. Fung. 1:42. *Venturia cupressina* Rehm, Kew Herb. no. 394. On Cupressus, Pinaceae; Myrceugenia, Myrtaceae. Spores 16 x 6 μ ; paraphyses hyaline, delicate. Conidia: *Asterostomella*.

2. *Asterinella lembosioides* Doidge, Trans. Roy. Soc. So. Afr. 8:267. 1920. On Balladyna and Meliola, fungi; Plectronia, Rubiaceae. Ascomata 200-240 μ or 280-320 x 160-240 μ , asci 33-43 x 17-20 μ , spores 15-17 x 8.5-10 μ .

3. *Asterinella leptotheca* (Speg.) Theiss., Ann. Myc. 10:174. 1912. *Asterina leptotheca* Speg., Fungi Puigg. no. 351, Bol. Acad. Nac. Ci. Cordoba 11:563. 1889. Syll. Fung. 9:386. 1891. *Mycrothyrium confluens* Pat., Bull. Boiss. p. 72. 1895; Syll. Fung. 11:380; Broteria 10:111. 1912. *Seynesia solani* (Speg.) Rehm, Hedw. 37:327. 1898. On Hirea, Malpighiaceae; Solanum, Cestrum, Solanaceae. Ascomata 100-200 μ , asci 45 x 16 μ , spores 14-18 x 5-8 μ . Öst. Bot. Zeitschr. 62:218. 1912.
4. *Asterinella drymidis* (Lév.) Speg., Bol. Acad. Nac. Ci. Cordoba 25:92. 1921. *Lembosia drymidis* Lév., Ann. Sci. Nat. ser. 3, 3:58. 1845. *Asterina compacta* Lév., Ann. Sci. Nat. ser. 3, 3:60. 1845. On Drymis, Magnoliaceae. Asci ovoid, 40-45 x 25 μ , spores 18-20 x 6-7 μ . Syll. Fung. 2:743; Abh. K. K. Zool.-Bot. Ges. 7:22. 1913; Ann. Myc. 11:425. 1913.
5. *Asterinella stuhlmanni* (Henn.) Theiss., Broteria 10:120. 1912. *Asterina stuhlmanni* Henn., Notisbl. Bot. Gart. p. 239. 1903. On Ananassa, Bromeliaceae. Ascomata 120-140 μ , asci 25-32 x 18-24 μ , spores 16-19 x 8 μ . Syll. Fung. 17:881; Ann. Myc. 21:104. 1923.
6. *Asterinella hippeastri* Ryan, Mycologia 16:188. 1924. On Hippeastrum and Hippocratea, Hippocrataceae; Amaryllidaceae. Ascomata 120 μ , asci 19-21 x 29-31 μ , spores 19 x 5-7 μ . N. Y. Acad. Sci. 8:21. 1926.
7. *Asterinella epidendri* (Rehm) Theiss., Broteria 10:180. 1912. *Seynesia epidendri* Rehm, Hedw. 39:228. 1904; Syll. Fung. 16:641. On Epidendrum, Orchidaceae. Ascomata 150-180 μ , asci 60 x 15 μ , spores 16-20 x 8 μ . Öst. Bot. Zeitschr. 63:124. 1913.
8. *Asterinella gracilis* Syd., Ann. Myc. 12:559. 1914. On Derris, Leguminosae. Ascomata 90-140 μ , or 180-230 x 70-90 μ , asci 20-28 x 18-22 μ , spores 18-20 x 7-8 μ . Syll. Fung. 24:481.
9. *Asterinella brasiliensis* (Wint.) Theiss., Ann. Myc. 10:173. 1912. *Asterina brasiliensis* Wint., Hedw. 32:101. 1892. Syll. Fung. 11:255. *Microthyrium disiunctum* Rehm, Ann. Myc. 6:123. 1908. *Asterina disiuncta* v. Höhn., in herb. *Opeasterinella brasiliensis* Speg., Bol. Acad. Nac. Ci. Cordoba 23:498. 1919. On Calliandra, Leguminosae; Solanum, Solanaceae. Ascomata 200-250 μ , asci 80-100 x 20-23 μ , spores 18-22 x 9-12 μ . Syll. Fung. 22:518; Öst. Bot. Zeitschr. 62:276. 1912.
10. *Asterinella palawanensis* Syd., Philipp. Jour. Sci. 9:182. 1914. On Plectronia, Rubiaceae. Ascomata 200-350 μ , asci 45-55 x 24-34 μ , spores 18-24 x 7-8.5 μ . Syll. Fung. 24:484.
11. *Asterinella lugubris* Syd., Philipp. Jour. Sci. 8:491. 1913. On Ixora, Rubiaceae. Ascomata 100-140 or 600 x 70-120 μ , asci 35-50 x 24-26 μ , spores 18-24 x 8-9 μ . Syll. Fung. 24:483.
12. *Asterinella mindanaensis* Syd., Ann. Myc. 21:103. 1923. On Arthrophyllum, Araliaceae. Ascomata 220-300 μ , asci 56-90 x 18-22 μ , spores 20-24 x 7-9 μ .

13. *Asterinella dissiliens* Syd., Ann. Myc. 22:425. 1924. On *Elaeodendron*, Celastraceae. Ascomata 130-200 μ , asci 45-55 x 25-35 μ , spores 21-24 x 9-10 μ .

14. *Asterinella creberrima* Syd., Ann. Myc. 15:247. 1917. *Asterinella regesiana* Rehm, Ann. Myc. 16:247. 1918. On *Premna*, Verbenaceae. Ascomata 70-120 μ , asci 35-40 x 30-35 μ , spores 24-27 x 12-13 μ . Syll. Fung. 24:485.

15. *Asterinella sublibera* (Berk.) Theiss., Broteria 10:113. 1912. *Asterina sublibera* Berk., Fl. N. Zeal. 2:210; Syll. Fung. 1:43. 1882. On *Metrosideros*, Myrtaceae. Ascomata 250-340 μ , asci 70-75 x 20-22 μ , spores 25-27 x 10 μ .

16. *Asterinella puiggarii* (Speg.) Theiss., Broteria 10:116; Frag. brasil. no. 139; Ann. Myc. 10:1912. *Asterina puiggarii* Speg., Fungi Guar. II, no. 124, Bol. Acad. Nac. Ci. Cordoba 11:566. 1889; Syll. Fung. 1:43. 1882. *Asterella balansae* Speg. var. *macrospora* Speg., in herb. *Microthyrium cantarcirensense* Henn., Hedw. 41:300. 1902. Syll. Fung. 17:863. *Asterina serrensis* Henn., Hedw. 48:12. 1908; Syll. Fung. 24:463. *Asterina typhospora* Maire, Ann. Myc. 6:148. 1908. *Asterella verrucolosa* Syd., Ann. Myc. 2:168. 1904. *Asterina leopeoldina* Rehm, Ann. Myc. 5:521. 1907; Syll. Fung. 14:698. *Asterella missionum* Speg., Myc. Arg. IV no. 735. 1909. *Asterella glaziovii* Henn., Hedw. 36:217. 1897. Syll. Fung. 14:698. 1899. *Seynesia balansae* var. *myrtacearum* Speg., Fungi Guar., Pug. I, no. 297, Bol. Acad. Nac. Ci. Cordoba 11. 1889. On *Myrrhinii*, Myrtaceae. Ascomata 50-70 μ , asci 40-45 x 30-35 μ , spores 27-30 x 9-15 μ . Abh. K. K. Zool.-Bot. Ges. 7:89. 1913.

17. *Asterinella caaguazensis* (Speg.) Theiss., Frag. brasil. no. 141, Ann. Myc. 10:173. 1912. *Microthyrium caaguazense* Speg., Fungi Guar., Pug. I, no. 296; Syll. Fung. 9:1055. 1891; Öst. Bot. Zeitschr. 62:217. 1912. *Microthyrium concatenatum* Rehm, Hedw. 38:321. 1898; Syll. Fung. 14:687. *Calothyriolum caaguazense* Speg., Fungi Guar., Pug. I, no. 296. 1882. On *Myrrhinii*, Calyptranthes, Campomanesiae, Myrtaceae. Ascomata 150-200 μ , asci 65-26 x 25-12 μ , spores 27-30 x 9-15 μ . Syll. Fung. 17:884; Broteria 10:117. 1912; 11:7. 1913; Abh. K. K. Zool.-Bot. Ges. 7:37. 1913; Öst. Bot. Zeitschr. 62:276. 1912.

18. *Asterinella dysoxyli* Syd., Ann. Myc. 29:242. 1931. On *Dysoxylon*, Meliaceae. Ascomata 80-200 μ , asci 35-50 μ , spores 24-32 μ .

19. *Asterinella uleana* (Pazs.) Theiss., Ann. Myc. 10:175. 1912. *Asterina uleana* Pazs., Hedw. 32:104. 1892; Syll. Fung. 11:255. *Seynesia megas* Rehm, Hedw. 37:325. 1898; Syll. Fung. 16:640. *Seynesia megas* var. *macrospora* Starb., Asco. I, Regm. Exped. Fung. Paul. Rev. Mus. La Plata 15:27. 1896; Syll. Fung. 22:540. 1913. *Asterina dispar* Speg. var. *paraphysata* Speg., in herb. On *Styrax*, Styraceae; *Myrcia*, Myrtaceae;

Chrysobalanus, Rosaceae; *Brysonima*, Malpighiaceae. Ascomata 400-450 μ , asci 85-90 x 35-38 μ , spores 35-42 x 16-20 μ .

20. *Asterinella hydnocarpi* Yates, Philipp. Jour. Sci. 12:372. 1917. (Corr. *Asterinella hydnocarpiae*). On *Hydnocarpus*, Flacourtiaceae. Ascomata 300-400 μ , asci 70 μ , spores 40-50 x 25-28 μ . Syll. Fung. 24:481.

21. *Asterinella phoradendri* (Henn.) Theiss., Broteria 10:108. 1912. *Asterina phorodendri* Henn., Hedw. 48:12. 1908. On *Phoradendron*, Loranthaceae. Asci 50-95 x 40-50 μ , spores 30-40 x 20-24 μ . Syll. Fung. 24:458.

22. *Asterinella gmeliae* Sacc. Notae Myc. 20. Nuova Giour. Bot. Ital. 23:199. 1916. On *Gmelia*, Verbenaceae. Ascomata 160 μ , asci 60-80 or 80 x 65 μ , spores 38 x 14-16 μ . Syll. Fung. 24:485.

23. *Asterinella papayae* Frag. and Cif., Bol. de Real. Soc. Esp. de Hist. Nat. 25:443. 1925. On *Carica papaya*, Caricaceae. Estacion Agron. de Moca, ser. B, no. 14, p. 70.

41. POLYTHYRIUM Sydow

Annales Mycologici 27:64. 1929.

Type: *P. costaricense* Syd.

Characters: Free mycelium present, no hyphopodia, ascomata orbicular, stellate ostiole, paraphyses present, gelatinous, spores 2-celled.

1. *Polythyrium costaricense* Syd., Ann. Myc. 27:64. 1929. On *Picrammia*, Simarubaceae. Ascomata 100-250 μ , asci 38-55 x 12-20 μ , spores 15-18 μ long.

2. *Polythyrium parameriae* (Petr.) Ryan, n. comb. *Asterinella parameriae* Petr., Ann. Myc. 29:243. 1931. On *Parameria*, Apocynaceae. Ascomata 90-160 μ , asci 30-38 x 25-30 μ , spores 17-21 x 8-10 μ .

3. *Polythyrium microchita* (Syd.) Ryan, n. comb. *Asterinella microchita* Syd., Ann. Myc. 26:96. 1928. On *Nothophoebes*, Lauraceae. Ascomata 75-120 μ , asci 27-35 x 23-28 μ , spores 20-23 x 9-10 μ .

42. CLYPEOLINA Theissen

Annales Mycologici 15:419. 1917.

Type: *C. apus* Theiss.

Characters: No hyphopodia; dimidiate, ostiolate, no paraphyses; spores 2-celled, brown. Like *Clypeolella*.

1. *Clypeolina apus* (Theiss.) Theiss., l. c. *Clypeolella apus* Theiss., Centralbl. Bakt. Abt. 2. 34:234. 1912. On Bignoniaceae. Ascomata 85-140 μ , asci 42-56 x 22-30 μ , spores 18-20 x 6.5-9 μ .

43. PRILLIEUXINA Arnaud

Ann. École Nat. Agr. Montp. 16:161. 1918.

Type: *P. winteriana* (Pazs.) Arn.

Characters: Free mycelium, non hyphopodiate; hymenium simple, paraphysate; ascomata circular; spores 2-celled, dark.

The species are arranged in order of maximum spore length.

1. *Prillieuxina ixorae* (Ryan) Ryan, n. comb. *Asterinella ixorae* Ryan, Mycol. 16:189. 1924. On *Ixora*, Rubiaceae. Ascomata 89-112 μ , asci 14-17 x 9 μ , spores 9 x 2-7 μ .

2. *Prillieuxina mabae* (Stev. and Ryan) Ryan, n. comb. *Asterinella mabae* Stev. and Ryan, Bernice P. Bishop Mus. Bul. 19:75. 1925. On *Maba*, Ebenaceae. Ascomata 162 μ , asci 23 x 36 μ , spores 12 x 5 μ .

3. *Prillieuxina flexuosa* (Wint.) Ryan, n. comb. *Asterinella flexuosa* (Wint.) Theiss., Broteria 10:104. 1912. *Asterella flexuosa* Wint., Hedw. 32:101. 1892; Syll. Fung. 11:256. On *Calliandra*, Leguminosae. Ascomata 230-300 μ , asci 24-27 x 14-16 μ , spores 14 x 3.5 μ .

4. *Prillieuxina distinguenda* (Syd.) Ryan, n. comb. *Asterinella distinguenda* Syd., Philipp. Jour. Sci. 8:492. 1913. On *Ixora*, Rubiaceae. Ascomata 150-225 x 100-170 μ , asci 20-35 x 15-19 μ , spores 12-14 x 5.5-6.5 μ . Syll. Fung. 24:484.

5. *Prillieuxina acokantherae* (Doidge) Ryan, n. comb. *Asterinella acokantherae* Doidge, Trans. Roy. Soc. So. Afr. 8:266. 1920. On *Acokanthera*, Apocynaceae. Conidial stage only on *Carissa*, Apocynaceae. Ascomata 90-115 μ , asci 26-35 x 13-17 μ , spores 3.5-5 x 13-17 μ .

6. *Prillieuxina lepidotricha* (Theiss.) Ryan, n. comb. *Asterinella lepidotricha* Theiss., Ann. Myc. 14:271. 1916. On leaves. Ascomata 100-130 μ , asci 45-50 x 30-33 μ , spores 16-17 μ . Syll. Fung. 24:426.

7. *Prillieuxina burchelliae* (Doidge) Ryan, n. comb. *Asterinella burchelliae* Doidge, Trans. Roy. Soc. So. Afr. 8:267. 1920. On *Burchellia*, Rubiaceae. Ascomata 100-120 μ , asci 27-37 x 16-20 μ , spores 13-17 x 5-6.6 μ .

8. *Prillieuxina manaosensis* (Henn.) Ryan, n. comb. *Asterinella manaosensis* Theiss., Broteria 10:115. 1912. *Asterella manaosensis* Henn., Hedw. 43:370. 1904; Syll. Fung. 17:882. On *Anonaceae*. Ascomata 180-250 μ , asci 50-80 x 12-18 μ , spores 13-18 x 4-6 μ .

9. *Prillieuxina cylindrotheca* (Speg.) Ryan, n. comb. *Asterinella cylindrotheca* Theiss., Broteria 10:114. 1912. *Asterina cylindrotheca* Speg., Fungi Puigg. no. 349. 1889; Syll. Fung. 9:386. 1891; Bol. Acad. Nac. Ci. Cordoba 11:561. 1889. *Asterina macularis* Syd., Ann. Myc. 2:168. 1904; Syll. Fung. 17:883. *Asterella macularis* Syd., Ann. Myc. 2:168. 1904. On *Eugenia*, *Myrceugenia*, *Myrtaceae*. Ascomata 120-180

μ , asci 50-80 x 18-20 μ , spores 14-19 x 6-8 μ , pseudoparaphysate. N. Y. Acad. Sci. 8:21. 1926.

10. *Prillieuxina venusta* (Syd.) Ryan, n. comb. *Asterinella venusta* Syd., Ann. Myc. 18:101. 1920. On Anaxagorea, Anonaceae. Ascomata 60-100 x 50-70 μ , asci 20-30 x 20 μ , spores 15-20 x 5-6 μ . Syll. Fung. 24:479.

11. *Prillieuxina systema-solare* (Mass.) Ryan, n. comb. *Asterinella systema-solare* Theiss., Broteria 10:180. 1912. *Asterina systema-solare* Mass., Kew Bull. p. 160. 1901; Syll. Fung. 17:880. *Seynesia banksiae* Henn., Hedw. 42:78. 1903; Syll. Fung. 17:867. *Didymosphaeria banksiae* Cke., Grev. 19:90. 1890. On Banksia, Rosaceae. Ascomata 90-100 μ , asci 50-55 x 12 μ , spores 16-20 x 7-9 μ . Ann. Myc. 10:180. 1912. Öst. Bot. Zeitschr. 63:101. 1913.

12. *Prillieuxina intensa* (Cke. and Mass.) Ryan, n. comb. *Asterinella intensa* Theiss., Broteria 10:120. 1912. *Asterina intensa* Cke. and Mass., Grev. 15:101. 1886; Syll. Fung. 9:382. On Osmanthus, Oleaceae; Eleaodondron, Celastraceae; Pisonia, Nyctaginaceae. Ascomata 125 μ , spores 15 x 8 μ , or 18-21 x 8-9 μ . Bernice P. Bishop Mus. Bul. 19:75, 1925; Mem. Dept. Agr. India 15:105. 1927.

13. *Prillieuxina capizensis* (Mendoza) Ryan, n. comb. *Asterinella capizensis* Mendoza, Philipp. Jour. Sci. 49:189. 1932. On Leucosyke, Urticaceae. Ascomata 95-200 μ , asci 31-39 x 31-36 μ , spores 19-22 x 9-10 μ .

14. *Prillieuxina woodiana* (Doidge) Ryan, n. comb. *Asterinella woodiana* Doidge, Trans. Roy. Soc. So. Afr. 8:266. 1920. On Cryptocarya, Lauraceae. Ascomata 150-160 μ , asci 33-37 x 27-30 μ , spores 20-23 x 10 μ . Conidia: Asterostomella.

15. *Prillieuxina amazonica* (Syd.) Ryan, n. comb. *Asterinella amazonica* Syd., Ann. Myc. 14:92. 1916. On Ramisia, Nyctaginaceae. Ascomata 100-160 or 250 x 80-120 μ , asci 32-40 x 20-35 μ , spores 20-24 x 9-11 μ . Syll. Fung. 24:483.

16. *Prillieuxina anamirtae* (Syd.) Ryan, n. comb. *Asterinella anamirtae* Syd., Ann. Myc. 12:558. 1914. On Anamirta, Memispermaceae. Ascomata 80-100 μ , asci 50-60 x 35-40 μ , spores 22-25 x 9-11 μ . Syll. Fung. 24:482; Ann. Myc. 29:244. 1931.

17. *Prillieuxina ramuligera* (Syd.) Ryan, n. comb. *Asterinella ramuligera* Syd., Philipp. Jour. Sci. 9:182. 1914. On Microdesmus, Euphorbiaceae. Ascomata 140-200 μ , asci 35-47 x 30-40 μ , spores 20-26 x 10-12 μ . Syll. Fung. 24:481.

18. *Prillieuxina quinta* (Rac.) Ryan, n. comb. *Asterinella quinta* (Rac.) Theiss., Broteria 10:105. 1912. *Asterina quinta* Rac. in Herb. Java. Host not known. Ascomata 100-140 μ , asci 36-45 or 35-40 x 50-60 μ , spores 22-27 x 10-12 μ .

19. *Prillieuxina dipterocarpi* (Syd.) Ryan, n. comb. *Asterinella dipterocarpi* Syd., Ann. Myc. 12:558. 1914. On Dipterocarpus, Diptero-

carpaceae. Ascomata 140-200 or 400 μ , asci 55-70 x 35-45 μ , spores 24-28 x 8-10 μ . Syll. Fung. 24:480; Ann. Myc. 29:244. 1931.

20. *Prillieuxina multilobata* (Wint.) Ryan, n. comb. *Asterinella multilobata* (Wint.) Theiss., Broteria 10:119. 1912. *Asterina multilobata* Wint., Hedw. 26:25. 1886; Syll. Fung. 11:255; Rabh. Fungi Europi 3438. *Seynesia multilobata* (Wint.) Rehm, Hedw. 28:245. 1899. On Malpighiaceae; Raumirta, Paumirtaceae; Paullinia, Sapindaceae. Ascomata 100-150 μ , asci 35-42 or 22 x 46 μ , spores 22-29 x 10-11 μ . Mycologia 16:189. 1924.

21. *Prillieuxina cryptocaryae* (Cke.) Ryan, n. comb. *Asterinella cryptocaryae* (Cke.) Theiss., Broteria 10:107. 1912. *Asterina cryptocaryae* Cke., in herb. On Cryptocarya, Lauraceae; Prunus, Rosaceae; Symplocaceae. Ascomata 250-300 μ , asci aparaphysate, spores 26-29 x 10-13 μ .

22. *Prillieuxina microspila* Syd., Philipp. Jour. Sci. 21:141. 1922. On Leucosyke, Urticaceae. Ascomata 150-200 μ , asci 35-50 x 25-40 μ , spores 21-24 x 9-10 μ .

23. *Prillieuxina winteriana* (Pazs.) Arn., l. c. *Asterina winteriana* Pazs., Hedw. 32:104. 1892. *Asterinella winteriana* (Pazs.) Theiss., Broteria 10:122. 1912. *Asterina anonicola* Henn., Hedw. 41:108. 1902. On Anona, Rollinia, Anonaceae; Castanopsis, Fagaceae. Ascomata 140-340 or 550 x 220 μ , asci 55-65 x 42-45 μ , spores 12-14 x 27-31 μ . Syll. Fung. 17:877; 11:255; Mem. Dept. Agr. India 15:107. 1927.

24. *Prillieuxina diaphana* (Syd.) Ryan, n. comb. *Asterinella diaphana* (Syd.) Theiss., Broteria 10:105. 1912. *Asterina diaphana* Syd., Leaflet Philipp. Bot. 4:1155. 1911. On Solanum, Solanaceae. Ascomata 100-200 μ , asci 35-55 x 35-42 μ , spores 28-30 x 12-15 μ . Syll. Fung. 24:472.

25. *Prillieuxina tjibodensis* (v. Höhn.) Ryan, n. comb. *Asterinella tjibodensis* v. Höhn. Sitz. K. Akad. Wiss. Wien 129:142. 1920. On leaves. Ascomata 200-300 μ , spores 32 μ long.

26. *Prillieuxina humiriae* (Henn.) Ryan, n. comb. *Asterinella humiriae* Theiss., Broteria 10:121. 1912. *Seynesia humiriae* Henn., Hedw. 44:65. 1905; Syll. Fung. 17:866. On Byronia, Aquifoliaceae: Humiria, Humiriaceae. Ascomata 200-250 μ , asci 40-50 μ , spores 26-32 x 12-15 μ . Mem. Dept. Agr. India 19:75. 1927; Ann. Myc. 10:186. 1912; Öst. Bot. Zeitschr. 63:123. 1913.

27. *Prillieuxina amboiensis* Syd., Philipp. Jour. Sci. 21:142. 1922. On Cordyline, Liliaceae. Ascomata 200-400 μ , asci 45-60 x 25-40 μ , spores 26-35 x 13-15 μ .

28. *Prillieuxina loranathi* Syd., Philipp. Jour. Sci. 21:141. 1922. *Asterinella loranathi* Syd., Philipp. Jour. Sci. 8:490. 1913. On Loranthus, Loranthaceae. Ascomata 140-180 μ , asci 45-60 x 32-45 μ , spores 26-34 x 14-16 μ . Syll. Fung. 24:482.

29. *Prillieuxina calotheca* (Pat. and Lag.) Ryan, n. comb. *Asterinella*

calotheca Theiss., Abh. K. K. Zool.-Bot. Ges. 7:117. 1913. *Asterina calotheca* Pat. and Lag. Champ de l'Equateur, Soc. Myc. Fr. 11:221. 1895. On leaves. Ascomata 300-400 μ , asci 80 x 40-50 μ , spores 28-32 x 15-16 μ . Syll. Fung. 14:697; Broteria 12:77. 1914.

30. *Prillieuxina luzonensis* (Syd.) Ryan, n. comb. *Asterinella luzonensis* Syd., Philipp. Jour. Sci. 8:491. 1913. On Shorea, Dipterocarpaceae. Ascomata 150-200 or 800 x 170 μ , asci 50-62 x 40-52 μ , spores 29-33 x 13-15 μ . Syll. Fung. 24:480.

31. *Prillieuxina calami* (Syd.) Ryan, n. comb. *Asterinella calami* Syd., Philipp. Jour. Sci. 9:182. 1914. On Calamus, Palmae. Ascomata 250-420 μ , spores 34-35 x 15-17 μ .

32. *Prillieuxina melastomacearum* Ryan, n. comb. *Asterinella melastomacearum* Ryan, Mycologia 16:189. 1924. On Melastomataceae. Ascomata 120-336 μ , asci 45-48 x 57-72 μ , spores 14-17 x 29-36 μ .

33. *Prillieuxina santiriae* (Syd.) Ryan, n. comb. *Asterinella santiriae* Syd., Ann. Myc. 15:248. 1917. On Santiria, Burseraceae. Ascomata 300-350 or 400 x 250-300 μ , asci 50-75 x 45-60 μ , spores 32-36 x 19-17 μ . Syll. Fung. 24:479.

34. *Prillieuxina clavispora* (Rehm) Ryan, n. comb. *Asterinella clavispora* (Rehm) Theiss., Broteria 12:76. 1914. *Seynesia clavispora* Rehm, Philipp. Jour. Sci. 8:190. 1913. On Alyxia, Apocynaceae. Ascomata to 200 μ , asci 30-60 x 25-30 μ , spores 35-40 μ long. Syll. Fung. 24:428.

35. *Prillieuxina antioquensis* (Toro) Ryan, n. comb. *Asterinella antioquensis* Toro, Jour. Dept. Agr. Puerto Rico 13:232. 1930. On Miconia, Melastomataceae. Ascomata 150-200 μ , asci 47-52 x 27-31 μ , spores 31-40 μ long.

36. *Prillieuxina saginata* (Syd.) Ryan, n. comb. *Asterinella saginata* Syd., Ann. Myc. 15:248. 1917. On Pinanga, Palmae. Ascomata 300-500 μ , asci 60-80 x 40-60 μ , spores 40-44 x 20-23 μ . Syll. Fung. 24:485.

37. *Prillieuxina asterinoides* (Pat.) Ryan, n. comb. *Asterinella asterinoides* Theiss., Öst. Bot. Zeitschr. 62:435. 1912. *Microthyrium asterinoides* Pat., Jour. Bot. 20:150. 1888. *Seynesia asterinoides* Sacc., Syll. Fung. 9:1064. 1891. On Gramineae. Ascomata 300-200 μ , asci 30-36 μ .

38. *Prillieuxina phoradendri* Ryan, n. comb. *Asterinella phoradendri* Ryan (not Theiss.), Mycologia 16:189. 1924. On Phoradendron, Loranthaceae. Ascomata 224-470 μ , asci 41-55 x 62-64 μ , spores 17 x 33-41 μ .

39. *Prillieuxina malabarensis* (Syd.) Ryan, n. comb. *Asterinella malabarensis* (Syd.) Theiss., Broteria 10:106. 1912. *Asterina malabarensis* Syd., Ann. Myc. 9:391. 1911; Syll. Fung. 24:444. On Pothus, Araceae. Ascomata 150-250 x 60-400 μ , asci 45-58 x 25-35 μ , spores 22-26 x 11-13 μ .

40. *Prillieuxina pterocelastri* (Doidge) Ryan, n. comb. *Asterinella*

pterocelastri Doidge, Bothalia 2:198. 1927. On *Pterocelastus*, Celastraceae. Ascomata 150-180 μ , asci 30-37 x 20-25 μ , spores 17-20 x 6.5-8 μ .

41. *Prillieuxina mimusopsidis* (Doidge) Ryan, n. comb. *Asterinella mimusopsidis* Doidge, Bothalia 1:80. 1920. On *Mimusops*, Sapotaceae. Ascomata 240-320 μ , asci 60-70 x 25-35 μ , spores 28-33 x 13-16.5 μ .

44. HALBANIELLA Theissen

Annales Mycologici 14:430. 1916.

Type: *H. javanica* (Rac.) Theiss.

Characters: Mycelium present, non-hyphopodiate, ascomata round, radiate, ostiolate, basal membrane brown, paraphyses present, spores hyaline, 4-5 celled.

Literature: Annales Mycologici 18:79. 1920.

1. *Halbaniella javanica* (Rac.) Theiss., l. c. *Heterochlamys javanica* Rac., Bol. Acad. Sci. Cracovie 1:381. 1909. On *Tetracera*, Dilleniaceae; *Heterochlamys*, Euphorbiaceae. Ascomata 200 μ , asci 14-16 x 68-75 μ , spores 4-6 x 22-28 μ . Syll. Fung. 24:503.

2. *Halbaniella portoricensis* (Speg.) Seaver and Toro, N. Y. Acad. Sci. 8:212. 1926. *Asteridium portoricense* Speg., Bol. Acad. Nac. Ci. Cordoba 26:348. 1922. *Asteridiellina portoricensis* (Speg.) Seaver and Toro, N. Y. Acad. Sci. 8:212. 1926. On *Ocotea*, Lauraceae. Ascomata 200-250 μ , asci 75-100 x 15-20 μ , spores 30-35 x 5-6 μ .

3. *Halbaniella linnaeae* Dearn., Fungi of Manitoba, 1929. On *Linnaea*, Caprifoliaceae.

45. BEELIA Stevens and Ryan

Bernice P. Bishop Museum Bul. 19:71. 1925.

Type: *B. suttoniae* Stev. and Ryan.

Characters: Free mycelium present, ascomata dimidiate, radiate, ostiolate, orbicular, asci globular, paraphysate, spores straw-colored, 6-celled.

1. *Beelia suttoniae* Stev. and Ryan, l. c. On *Suttonia*, Myrsinaceae. Ascomata 90-227 μ , asci 63-72 x 39-45 μ , spores 12-14 x 32-36 μ .

46. KRIEGERIELLA v. Höhnelt

Annales Mycologici 16:39. 1918.

Type: *K. mirabilis* v. Höhn.

Characters: Free mycelium present, non-hyphopodiate, paraphysate, spores brown, several celled.

1. *Kriegeriella mirabilis* v. Höhn., l. c. On *Pinus*, Pinaceae. Ascomata

100-150 x 100-160 μ , asci 60-80 x 32-40 μ , spores 30-35 x 9-10 μ . Syll. Fung. 24:432.

2. *Kriegeriella transiens* v. Höhn., *l. c.* On Pinus, Pinaceae. Ascomata 120-240 x 80-100 μ , asci 60-64 x 24-28 μ , spores 24-28 x 7-9 μ . Syll. Fung. 24:432.

47. PLATYPELTELLA Petrak

Annales Mycologici 27:62. 1929.

Type: *P. smilacis* Petr.

Characters: Ascomata dimidiate, basal membrane thin, spores brown, 3-4 celled, paraphysate.

1. *Platyptella smilacis* Petr., *l. c.* On Smilax, Liliaceae. Ascomata 180-250 μ , asci 70-100 x 18-25 μ , spores 23-25 x 11-15 μ .

48. YATESULA Sydow

Annales Mycologici 15:237. 1917.

Type: *Y. calami* Syd.

Characters: Ascomata dimidiate, radiate, many hymenia, polyascigerous, paraphysate, spores muriform, reddish.

1. *Yatesula calami* Syd., *l. c.* On Calamus, Palamae. Asci 35-55 x 9-12 μ , spores 10-13 x 2.5-3.5 μ . Syll. Fung. 24:505.

49. LEMBOSIELLA Saccardo

Sylloge Fungorum 9:1101. 1891.

Type: *L. polyspora* (Pat.) Sacc.

Characters: Like *Lembosia* but spores 1-celled.

Literature: *Mycologisches Centralblatt* 3:278. 1913. Theissen says the single species needs restudy.

1. *Lembosiella polyspora* (Pat.) Sacc., *l. c.* *Lembosia polyspora* Pat., Bull. Soc. Myc. Fr. 3:125, tab. 10, fig. 4. 1887. On Ochnaceae. Ascomata 0.5-1 mm. long, asci 33-40 x 23-30 μ , paraphysate, spores 10 x 6-7 μ .

50. LEMBOSIOPSIS Theissen

Annales Mycologici 11:436. 1913.

Type: *L. andromedae* (Tracy and Earle) Theiss.

Characters: Ascomata linear, paraphyses present, no hyphopodia, spores colorless, 2-celled.

1. *Lembosiopsis cactorum* (Tracy and Earle) Theiss., *l. c.* *Lembosia*

cactorum Tracy and Earle, Bull. Torr. Bot. Club 27:186. 1901. On *Opuntia*, Cactaceae. Ascomata 200-250 x 100-150 μ , asci 25-30 x 16-20 μ , spores 12 x 4 μ . Syll. Fung. 17:897.

2. *Lembosiopsis brevis* (Tracy and Earle) Theiss., l. c. *Lembosia brevis* Tracy and Earle, Bull. Torr. Bot. Club 27:185. 1901. On *Opuntia*, Cactaceae. Ascomata 100-175 x 70-80 μ , asci 20 x 16 μ , spores 8-10 x 4 μ . Syll. Fung. 17:897.

3. *Lembosiopsis andromedae* (Tracy and Earle) Theiss., l. c. *Lembosia andromedae* Tracy and Earle, Bull. Torr. Bot. Club 23:207. 1896. On *Andromeda*, Ericaceae. Ascomata 250-400 x 50-90 μ , spores 8-9 x 2.5-3 μ . Syll. Fung. 14:714.

4. *Lembosiopsis oleae* (Tracy and Earle) Theiss., l. c. *Lembosia oleae* Tracy and Earle, Bull. Torr. Bot. Club 23:207. 1896. On *Olea*, Oleaceae. Ascomata 400 x 80-100 μ , spores 12-15 x 4 μ . Syll. Fung. 14:714.

5. *Lembosiopsis eucalyptina* Petr. and Syd., Ann. Myc. 22:372. 1924. On *Eucalyptus*, Myrtaceae. Asci 28-42 x 12.5-15 μ , spores 9-12.5 x 4-5 μ .

51. PTYCHOPELTIS Sydow

Annales Mycologici 25:78. 1927.

Type: *P. roupalae* Syd.

Characters: Mycelium superficial, non-hyphopodiate, ascomata dimidiate, radiate, elongate, asci 8-spored, spores 1-septate, hyaline, paraphyses branched.

1. *Ptychopeltis roupalae* Syd., l. c. On *Roupala*, Proteaceae. Ascomata 350-500 μ or 75 x 300-400 μ , asci 50-100 x 18-24 μ , spores 17-24 μ long.

52. AULOGRAPHUM Libert

Pl. Crypt. Ard. exc. no. 272, Leodii. Cent. II, 1832.

Type: *A. hederæ* Lib.

Characters: Mycelium superficial, non-hyphopodiate, ascomata linear, radiate, paraphysate, spores hyaline, 2-celled. Though the genus is defined as paraphysate both paraphysate and aphanysate species have been placed in it and are here listed.

Literature: Ann. Myc. 15:364. 1917; 16:150. 1918; Saccardo, Genera Pyrenomycetes tab. 13, fig. 16; Oudemans, Champ. Pays Bas tab. 13, fig. 16; Rev. Pyren. Batav. tab. 13, fig. 16.

1. *Aulographum culmigenum* Ellis, Bull. Torr. Bot. Club 8:65. 1881. On *Andropogon*, Gramineae; *Miconia*, Melastomataceae. Asci 12-14 x 7-8 μ , spores 5 x 1.8-2 μ . Mycologia 16:189. 1924; N. Y. Acad. Sci. 8:21. 1926; Syll. Fung. 2:729.

2. *Aulographum donacis* Niessl, Thüm. Contr. Myc. Lusit. no. 511, Instituto rev. scient. e litterar Coimbra 27:16. 1879. On *Donax*, Marantaceae. Ascomata minute, asci 24-30 x 12-15 μ , spores 5-6 x 2.5-3.5 μ . Syll. Fung. 2:729. 1882.

3. *Aulographum confluens* Earle, Bull. Torr. Bot. Club 24:365. 1898. On *Rubus*, Rosaceae. Ascomata 300-800 x 40 μ , asci 25-30 x 4-5 μ , spores 6 x 3 μ . Syll. Fung. 16:659.

4. *Aulographum gaylussaciae* Rehm, Hedw. 37:296, tab. 10, fig. 3. 1898. On *Gaylussacia*, Ericaceae. Ascomata 120-180 x 60-70 μ , asci 18 x 11 μ , spores 6 x 3 μ . Syll. Fung. 16:660.

5. *Aulographum tropicale* Rehm, Hedw., 39:210. 1900. On Pteridophytes. Ascomata 150-300 μ , asci 20 x 8 μ , spores 8 x 3 μ . Syll. Fung. 16:660.

6. *Aulographum gracile* Ell. and Mart., North Amer. Pyrenomycetes, p. 678, 1892. On *Quercus*, Fagaceae. Ascomata 60-70 μ , asci 20-25 x 10-12 μ , spores 7-8 x 3-3.5 μ . Syll. Fung. 11:386.

7. *Aulographum fimbriatum* Sacc., Notae Myc. 23:68. (Acc. Veneto-trent.) 1917. On *Daemonoropsis*, Palmae. Ascomata 200-300 x 50-60 μ , asci 25-30 x 6.5-7.5 μ , spores 7-8 x 2-3 μ . Syll. Fung. 24:438.

8. *Aulographum inconspicuum* Rehm, Hedw. 37:297. 1898. On *Myrti*, Myrtaceae. Ascomata 100 x 20 μ , asci 20 x 15 μ , spores 9 x 3 μ . Syll. Fung. 16:660.

9. *Aulographum validivianum* Speg., Fungi Chilensis, p. 110, 1910. On *Rubus*, Rosaceae. Ascomata 250-500 x 40-50 μ , asci 20-25 x 10-12 μ , spores 8-10 x 2.5 μ . Syll. Fung. 22:558.

10. *Aulographum quadriae* Berk., Grev. 22:15. 1893. On *Quadria*, Proteaceae. Ascomata 500 μ long, asci clavate, spores 8-10 x 4-5 μ . Syll. Fung. 11:386.

11. *Aulographum myrtaceae* Theiss., Ann. Myc. 16:187. 1918. On *Campomanesia*, Myrtaceae. Ascomata 180-240 x 35-50 μ , asci 24-28 x 14-16 μ , spores 8-10 μ . Syll. Fung. 24:437.

12. *Aulographum eucalypti* Cke. and Mass., Grev. 18:6. 1889. On *Eucalyptus*, Myrtaceae. Spores 9-10 x 4 μ . Syll. Fung. 9:1102.

13. *Aulographum bambusinum* Petr., Ann. Myc. 29:221. 1931. On *Bambusa*, Gramineae. Ascomata 1 mm. x 50-100 μ , asci 20-28 x 10-15 μ , spores 7-10 x 3-3.5 μ .

14. *Aulographum donaciola* Speg., Ann. Mus. Nac. Buenos Aires 19:441. 1909. On *Arundo*, Gramineae. Ascomata 150-200 x 75-100 μ , asci 30-35 x 12 μ , spores 10-12 x 5-6 μ . Syll. Fung. 22:558.

15. *Aulographum microthyrioideum* Rehm, Hedw. 39:209, tab. 11, fig. b. 1904. On leaves. Ascomata 140-300 x 50 μ , asci 20 x 10 μ , spores 10-12 x 3.5 μ . Syll. Fung. 16:660.

16. *Aulographum atro-maculans* Penz. and Sacc., Malpighia 11:527.

1897. On *Palmae*. Ascomata 400-500 μ , asci 25-30 x 8-9 μ , spores 12 x 4 μ . Syll. Fung. 14:711; Penz. and Sacc., Icon. F. Jav. tab. 42, fig. 1.

17. *Aulographum chusqueae* Speg., *Fungi Chilensis*, p. 109, 1910. On *Chusquea*, *Gramineae*. Ascomata 600-1000 x 30-80 μ , asci 25-28 x 14-18 μ , spores 10-12 x 3-4 μ . Syll. Fung. 22:558.

18. *Aulographum proteacium* Rodway. On *Cenarrhenes*, *Proteaceae*. Spores 14 x 6 μ . Syll. Fung. 24:1113. 1926.

19. *Aulographum melioides* Cke. and Mass., *Grev.* 18:6. 1889. On *Mammea*, *Guttiferae*. Spores 12-14 x 7-8 μ . Syll. Fung. 9:1101; N. Y. Acad. Sci. 8:21. 1926.

20. *Aulographum hederæ* Lib., *Pl. Crypt. Ard.*, fasc. 3, no. 272, 1834. *Aylographum vagum* Desm., *Pl. Crypt.* 10; *Ann. Sci. Nat.*, ser. 2, 19:362. 1843. *Hysterium micrographum* De Not., *Micr. Ital.*, Dec. 4, fig. 3. 1842. On *Hedera*, *Araliaceae*; *Olea*, *Phillyreae*, *Oleaceae*; *Ilicium*, *Magnoliaceae*; *Photinia*, *Rosaceae*; *Rhododendron*, *Ericaceae*. Asci 30-33 x 13 μ , spores 12-14 μ long. *Var. photiniae* Sacc., *Mich.* 1:54. 1878. Asci 23-32 x 13 μ , spores 15-17 x 3.5-4 μ . *Var. oleae* Sacc., *l. c.* Asci 30 x 8-9 μ , spores 10-12 x 2.5 μ . Syll. Fung. 2:727; *Ann. Epiphyties* 16:287. 1930; *Jour. Bot.* 73:103. 1935.

21. *Aulographum arundinariae* Cke., *Grev.* 14:14. 1885. On *Arundinaria*, *Gramineae*. Ascomata 1-2 mm. long, spores 13-15 x 5 μ . Syll. Fung. 9:1102.

22. *Aulographum blechnicola* Rehm, *Hedw.* 39:210. 1904. On *Blechnum*, *Acanthaceae*. Ascomata 180-200 x 60 μ , asci 30 x 20 μ , spores 15 x 5 μ .

23. *Aulographum maximum* Mass., *Bull. Misc. Inform. Roy. Gard. Kew*, p. 177, 1899. On *Imperata*, *Gramineae*. Ascomata linear, asci 90-100 x 12-14 μ , spores 17-18 x 5-6 μ . Syll. Fung. 16:660.

24. *Aulographum pandani* Cke., *Grev.* 5:17. 1876. On *Pandanus*, *Pandanaceae*. Ascomata minute, asci ovate or pyriform, spores 20 x 10 μ . Syll. Fung. 2:729.

25. *Aulographum cestri* Ryan, *Mycologia* 16:190. 1924. On *Cestrum*, *Solanaceae*. Ascomata 26-29 x 96-120 μ , asci 19-26 x 24-31 μ , spores 17-20 x 5-7 μ .

26. *Aulographum euryae* Syd., *Mem. Herb. Boiss.* no. 4, p. 5. 1900. On *Eurya*, *Theaceae*. Ascomata 125-250 μ , asci 50-60 x 9-11 μ , spores 18-20 x 4-5 μ . Syll. Fung. 16:659.

27. *Aulographum juruanum* Henn., *Fungi Amaz.* 3:382. 1904. On *Rollinia*, *Anonaceae*. Ascomata 150-180 x 100-140 μ , asci 50-60 x 35-50 μ , spores 25-30 x 10-14 μ . Syll. Fung. 17:895.

28. *Aulographum melaspileoides* Rehm, *Ber. Bayer Bot. Ges.* 13:103. 1912. On *Vaccinium*, *Ericaceae*. Ascomata 100 x 50 μ , asci 20-30 x 6-8 μ , spores 40 x 12-14 μ . Syll. Fung. 24:437.

29. *Aulographum subconfluens* Peck, 28 Report State Mus. N. Y. 1876. On stems. Spores 7.5-10 μ long, 1-septate (?).

In the following no measurements were given.

30. *Aulographum spilomoides* Ces., Myc. Born., Atti Acc. Sci. Napoli 8:14. 1880. On leaves. Ascomata oval to linear. Syll. Fung. 2:731.

31. *Aulographum intricatum* B. and B., Fungi Ceylon no. 1150, Jour. Linn. Soc. 14, tab. 9, fig. 50. 1875. On Pandanus, Pandanaceae. Syll. Fung. 2:731. 1886.

32. *Aulographum ciliatum* B. and C., Cuban Fungi no. 730. 1869. On *Clusia*, Guttiferaceae. Syll. Fung. 2:731.

33. *Aulographum canepae* De Not., Recl. Pir. p. 492. On *Thymus*, Labiatae. Asci clavate-obovate, spores ovoid. Syll. Fung. 2:729.

34. *Aulographum bromi* Berk., Crypt. Anar. p. 62, fig. 9; De Not. Pir. Ister. p. 32. On *Bromus*, Gramineae. Syll. Fung. 2:730.

53. CIRSOSIA Arnaud

Ann. École Nat. Agr. Montp. 16:123. 1918.

Type: *C. manaosensis* (Henn.) Arn.

Characters: Hyphopodia intercalary, paraphyses present, spores dark, 2-celled, ascomata linear.

1. *Cirsosia manaosensis* (Henn.) Arn. *l. c.* *Lembosia manaosensis* Henn., Hedw. 43:265. 1904. Syll. Fung. 17:898. On Malpighiaceae. Ascomata 300-400 x 200-250 μ , asci 55-65 x 45-50 μ , spores 25-35 x 13-17 μ . Syll. Fung. 24:497.

54. CIRSOSIELLA Arnaud

Ann. École Nat. Agr. Montp. 16:127. 1918.

Type: *C. transversalis* (Syd.) Arn.

Characters: Like *Cirsosia*, but aparaphysate.

1. *Cirsosiella transversalis* (Syd.) Arn., *l. c.* *Morenoella transversalis* Theiss., Ann. Myc. 11:457. 1913. *Asterina transversalis* Syd., Leaflet Philipp. Bot. 6:1542. 1911. On *Daemonorops* and *Calamus*, Palmae. Ascomata 500-900 x 180-250 μ , asci 60-80 x 50-60 μ , spores 40-50 x 18-22 μ .

2. *Cirsosiella globulifera* (Pat.) Arn., *l. c.* *Lembosia globulifera* Theiss., Jour. Bot. 4:65, fig. 9. 1890. Syll. Fung. 9:1108. *Asterina globulifera* Pat., Bul. Soc. Myc. Fr. 14:155. 1898. Syll. Fung. 16:648. On *Calamus*, Palmae. Ascomata 900-1000 x 500-600 μ , asci 40-45 μ , spores 30 x 10-13 μ . Ann. Myc. 11:441. 1913.

3. *Cirsosiella irregularis* (Syd.) Arn. *l. c.* *Morenoella irregularis*

Theiss., Ann. Myc. 11:458. 1913. *Asterina irregularis* Syd., Leaflet Philipp. Bot. 6:1540. 1911. *Halbanina irregularis* Arn., Ann. École Nat. Agr. Montp. 16:163. 1918. On *Vatica*, Dipterocarpaceae. Ascomata $1100 \times 200\text{--}300 \mu$, asci $60\text{--}80 \times 50\text{--}60 \mu$, spores $32\text{--}40 \times 15\text{--}16 \mu$.

55. LEMBOSIA Lévillé

Annales Sciences Naturelles, ser. 3, 3:58. 1845.

Type: *L. tenella* Lév.

Characters: Mycelium present, hyphopodiate, ascomata radiate, linear, paraphysate, spores 2-celled dark.

Literature: Ann. Myc. 11:425. 1913.

1. *Lembosia morotoni* Petr. and Cif., Ann. Myc. 30:195. 1932. On *Didymopana*, Araliaceae. Ascomata $180\text{--}450 \mu$, asci $28\text{--}35 \times 14\text{--}20 \mu$, spores $5\text{--}7 \times 1.5\text{--}2 \mu$.

2. *Lembosia glonioidea* Sacc., Bull. Orto Bot. Napoli 6:53. 1921. On *Hevea*, Euphorbiaceae. Ascomata $330\text{--}600 \times 90 \mu$, asci $45\text{--}50 \times 6\text{--}6.5 \mu$, spores $8\text{--}9 \times 3 \mu$. Syll. Fung. 24:492.

3. *Lembosia microtheca* Theiss., Beih. Bot. Centralbl. 27:44. 1910. On *Goeppertia*, Gentianaceae; *Cryptocarya*, Lauraceae; *Marantaceae*. Ascomata $180\text{--}300 \times 70\text{--}90 \mu$, asci $25\text{--}30 \times 9\text{--}11 \mu$, spores $9\text{--}10 \times 2.5\text{--}3 \mu$. Syll. Fung. 22:563.

4. *Lembosia cifferrii* (Petr. and Cif.) Ryan n. name. On *Ocotea*, Lauraceae. Ascomata $250\text{--}750 \times 100\text{--}180 \mu$, asci $19\text{--}23 \times 10\text{--}13 \mu$, spores small. This fungus was placed by the authors in *Lembosia microspora* Chard. The original description says that *L. microspora* is non-hyphopodiate, so it has since been placed in the genus *Echidnodes*. Petrak and Cifferri say, "Diese Art ist durch die meist gegenständigen, stumpf und verlängert zylindrisch-kegelformigen Hyphopodien gut charakterisiert und gleich kenntlich." Clearly the fungus is not that of Chardon. Therefore we have adopted the name *L. cifferrii* for this fungus. Ann. Myc. 30:195. 1932.

5. *Lembosia similis* (Bres.) Theiss., Ann. Myc. 13:435. 1915. *Asterina similis* Theiss., Ann. Myc. 11:435. 1913. *Lembosia similis* Bres., in Rick. Fungi Austro-Amer. no. 60. On *Myrtaceae*. Ascomata $180\text{--}300$ or $450 \times 200 \mu$, asci $32\text{--}47 \times 10\text{--}14 \mu$, spores $10 \times 4 \mu$.

6. *Lembosia maculare* (B. and B.) Theiss., Ber. Deutsch. Botan. Ges. 35:250. 1917. *Aulographum maculare* B. and B., Ann. Mag. Nat. Hist. 8:451. 1861. On *Bromeliaceae*. Spores $12\text{--}12.5 \times 3 \mu$. Syll. Fung. 2:730.

7. *Lembosia luzulae* (Lib.) v. Höhn., Ann. Myc. 15:366. 1917. *Aulographum luzulae* De Not., Pir. Istr. p. 30; Duby, Hyst. p. 38, tab. 3,

fig. 17. On *Luzula*, Juncaceae. Ascomata 150-200 x 50-80 μ , asci 20-24 x 12-15 μ , spores 9-12 x 5-5.5 μ . Syll. Fung. 2:728.

8. *Lembosia iliciicola* Tracy and Earle, Bull. Torr. Bot. Club 21:177. 1895. On *Ilicium*, Magnoliaceae. Ascomata 200-350 x 80-100 μ , asci 3-5 x 14-18 μ , spores hyaline then sub-colored, 10-13 x 5 μ . Syll. Fung. 14:712.

9. *Lembosia eucalypti* Stev. and Dixon, Bernice P. Bishop Mus. Bul. 19:75. 1925. On *Eucalyptus*, Myrtaceae. Asci 34 x 4-6 μ , spores 11-14 x 2-4 μ , hyaline—possibly immature.

10. *Lembosia microcarpa* Syd., Ann. Myc. 15:248. 1917. On *Calamus*, Palmae. Ascomata 200-400 x 50-100 μ , asci 23-27 x 16-20 μ , spores 11-14 x 7 μ . Syll. Fung. 24:494.

11. *Lembosia modesta* Theiss., Ann. Myc. 11:511. 1913. On *Araucaria*, Araucariaceae. Ascomata 170-250 x 60-90 μ , asci 30-40 x 20-24 μ , spores 12-14 x 7 μ . Syll. Fung. 24:492.

12. *Lembosia juncinum* (Lib.) v. Höhn., Ann. Myc. 15:366. 1917. *Aulographum juncinum* Lib., De Not. Pir. Istr. p. 31, tab. 3, fig. 19; Duby, Hyst. p. 39, tab. 2, fig. 20. On *Juncus*, Juncaceae. Ascomata 80-500 x 120 μ , asci 28 x 12-14 μ , spores 14 x 5 μ . Syll. Fung. 2:730; Ann. Epiphyties 16:286. 1921.

13. *Lembosia inconspicua* Syd., Philipp. Jour. Sci. 9:183. 1914. On *Guioa*, Sapindaceae. Ascomata 150-350 x 100-150 μ , asci 26-32 x 14-20 μ , spores 11-15 x 3.5-5 μ . Syll. Fung. 24:496.

14. *Lembosia rolfsii* Horne, Bull. Torr. Bot. Club 31:69. 1905. On *Vanilla*, Orchidaceae. Ascomata 350-1000 x 160 μ , asci 20-40 x 8-15 μ , spores 10-16 x 4-5 μ . Syll. Fung. 22:563.

15. *Lembosia decolorans* Syd., Ann. Myc. 12:561. 1914. On *Quercus*, Fagaceae. Ascomata 300-450 x 140-170 μ , asci 40-55 x 16-22 μ , spores 13-16 x 5.5-7 μ . Syll. Fung. 24:492.

16. *Lembosia natalensis* Doidge, Trans. Roy. Soc. So. Afr. 8:268. 1920. On Myrtaceae ? Ascomata 300-500 x 140-160 μ , asci 30-34 x 20-24 μ , spores 15-16 x 6-7 μ .

17. *Lembosia opaca* Speg., Ann. Myc. 11:438. 1913. On *Rapanea*, Myrsinaceae. Ascomata 250-340 x 140-170 μ , asci 32-40 x 17-22 μ , spores hyaline, later becoming brown, 16 x 5.5 μ , paraphyses typical. Theissen (85) p. 438, says, "mit sparlichen kurz zylindrischen Hyphopodia, 8 x 4-5 μ , besetz." *Lembosia nobilis* Speg., Fungi Guar. nonn. no. 129, p. 45. *Lembosia lophiostomacea* Starb., Ark. f. Bot. 2:8, fig. 16-18. 1904. Syll. Fung. 9:1105; 11:387; 17:900; Hedw. 37:tab. 9, fig. 8, 1898; Ann. École Nat. Agr. Montp. 16:135. 1918.

18. *Lembosia patouillardii* Sacc. and Syd., Syll. Fung. 14:715. *Lembosia philodendri* Henn., Hedw. 43:89. 1904. Ann. Myc. 11:448. 1913. *Lembosia orbicularis* Pat. (not Wint.), Jour. Bot. 27:168. 1889. Syll.

Fung. 9:1108. On *Dracaena*, Liliaceae; *Psidium*, Myrtaceae; *Philodendron*, Araceae; *Coccoloba*, Polygonaceae. Ascomata 0.5-0.9 x 0.17-0.2 mm., spores 16-18 x 6-7 μ . N. Y. Acad. Sci. 8:23. 1926; *Mycologia* 16:190. 1924; *Ann. Myc.* 25:78. 1927.

19. *Lembosia incisa* (Syd.) Theiss., *Ann. Myc.* 11:443. 1913. *Asterina incisa* Syd., *Ann. Myc.* 9:390. 1911. On *Webera*, Melastomataceae. Ascomata 300-500 μ long, asci 32-44 x 16-21 μ , spores 13-17 x 6-8 μ . *Syll. Fung.* 24:460.

20. *Lembosia vriesiae* (Rehm) v. Höhn., *Ann. Myc.* 15:371. 1917. *Micropeltis vriesiae* Rehm, *Ann. Myc.* 5:531. 1907. *Aulographum maculare* B. and B. var. *stellulata* Rehm, *Hedw.* 27:297, tab. 9, fig. 5. 1898. On Bromeliaceae. Ascomata 1 mm. x 60 μ , asci 40-50 x 22-24 μ , spores 22-24 x 7-9 μ .

21. *Lembosia tenella* Lév., *Ann. Sci. Nat. ser. 3 Bot.* 3:58. 1845. *Lembosia coccolobae* Earle, N. Y. Bot. Gard. Bul. 3:301. 1903. On *Coccoloba*, Polygonaceae; *Eugenia* Myrtaceae. Ascomata 200-250 x 160-180 μ , or 300-350 μ long, or T-formed, 450-500 x 120-150 μ , asci 40 x 25-30 μ , spores 17-22 x 5-6 μ . It has been suggested by Petrak and Ciferri (37) p. 165, that since the original specimen of *Lembosia tenella* Lév. has been destroyed *L. coccolobae* Earle be kept as the type for the genus. We suggest that the specimens from the Nicaragua collection (*Ann. Myc.* 11:426, tab. 20, fig. 25. 1913) be used as type, as they are in good condition. *Syll. Fung.* 2:742, 22:562; *Mycologia* 13:282. 1912; 16:190. 1924; *Ann. Myc.* 28:384. 1930.

22. *Lembosia longissima* Rac., *Parasit. Algen und Pilze Javas* 3:29. 1900. On *Neprolepis*, Pteridophyta. Ascomata 1-4 mm. x 30-40 μ , asci 38-44 x 17 μ , spores 15-17 x 5-6 μ . This is a questionable *Lembosia*. The original description makes no mention of hyphopodia. *Syll. Fung.* 16:684.

23. *Lembosia hormosiana* Sacc., *Bull. Orto Bot. Nap.* 6:52. 1921. On *Hormosia*. Ascomata 235-400 x 90 μ , asci 35-40 x 18-20 μ , spores 17-16 x 6.5-5 μ . *Syll. Fung.* 24:493.

24. *Lembosia congesta* Wint., *Flora* 42:9. 1884. *Syll. Fung.* 9:1105. On *Carissa*, Apocynaceae. Ascomata 500-800 x 180-220 μ , asci 60-70 x 21-26 μ , spores 17-18 x 7-9 μ . Questionable species. The original description does not give hyphopodia. *Trans. Roy. Soc. So. Afr.* 8:268. 1920.

25. *Lembosia sophorae* (Rehm) Ryan, n. comb. *Lembosia graphoides* S. and B. var. *sophorae* Rehm, *Ann. Myc.* 6:486. 1908. Exsiccati: Rehm, *Ascom.* p. 4168, no. 1780. On *Sophora*, Leguminosae. Ascomata 160-300 x 120 μ , asci 40 x 22-26 μ , spores 16-18 x 5-7 μ . *Ann. Myc.* 11:450. 1913.

26. *Lembosia sepotae* Ryan, *Mycologia* 16:191. 1924. On *Calophyllum*, Sepotaceae. Ascomata 224-616 μ , asci 17-27 x 29-34 μ , spores 7-9 x 14-19 μ . N. Y. Acad. Sci. 8:23. 1926.

27. *Lembosia philippinensis* Syd., *Ann. Myc.* 15:249. 1917. On

Randia, Rubiaceae. Ascomata 250-600 x 150-190 μ , asci 35-46 x 20-24 μ , spores 17-19 x 7-6 μ . Syll. Fung. 24:496.

28. *Lembosia piriensis* Doidge, *Bothalia* 1:78. 1920. On *Trichocladus*, Hamamelidaceae. Ascomata 300-400 x 190-240 μ , asci 37-40 x 20-24 μ , spores 17-20 x 6-7 μ .

29. *Lembosia poasensis* Syd., *Ann. Myc.* 23:397. 1925. On *Chamaedorea*, Palmae. Ascomata 300-1000 x 100-180 μ , asci 36-48 x 16-20 μ , spores 17-20 μ .

30. *Lembosia radiata* Doidge, *Trans. Roy. Soc. So. Afr.* 8:269. 1920. On Leguminosae. Ascomata 240-300 x 60-160 μ , asci 42-45 x 18-23 μ , spores 17-20 x 8-10 μ .

31. *Lembosia brenesii* Petr., *Ann. Myc.* 27:60. 1929. On *Mollinedia*, Monimiaceae. Ascomata 300-600 x 120-230 μ , asci 35-45 x 17-23 μ , spores 18-20 x 7-8 μ .

32. *Lembosia pavettae* Theiss., *Ann. Myc.* 11:429. 1913. On *Pavetta*, Rubiaceae. Ascomata to 700 μ long, asci 65 x 10-12 μ , spores 18-21 x 6-8 μ . *Var. luzonensis* Syd., *Ann. Myc.* 15:249. 1917. Ascomata 300-600 x 180-250 μ , asci 35-50 x 20-25 μ , spores 18-21 x 7-9 μ . Syll. Fung. 24:495.

33. *Lembosia rapanae* Ryan, *Mycologia* 16:191. 1924. On *Rapanea*, Myrsinaceae. Ascomata 190-336 x 616-672 μ , asci 29-36 x 12 μ , spores 21 x 7 μ .

34. *Lembosia rubiacearum* Arn., *Ann. École Nat. Agr. Montp.* 16:61. 1918. On Rubiaceae. Spores 21.5 x 14.5 μ . Syll. Fung. 24:496.

35. *Lembosia anorarum* Petr. and Cif., *Ann. Myc.* 30:193. 1932. On *Anona*, Anonaceae. Ascomata 200-500 x 80-120 μ , asci 38-46 x 25-35 μ , spores 17-22 x 9-10 μ .

36. *Lembosia pittierii* Syd., *Ann. Myc.* 28:146. 1930. On *Sickingia*, Rubiaceae. Ascomata 180-750 x 120-200 μ , asci 40-50 x 22-30 μ , spores 18.5-23 x 8-10 μ .

37. *Lembosia eugeniae* Rehm, *Philipp. Jour. Sci.* 8:261. 1913. On *Eugenia*, Myrtaceae. Ascomata 150-200 x 100 μ , asci 60 x 30 μ , spores 20-22 x 8-9 μ . Syll. Fung. 24:494; *Ann. Myc.* 20:72. 1922.

38. *Lembosia miconiicola* Arn., *Ann. École Nat. Agr. Montp.* 16:131, tab. 17, fig. 20. 1918. *Lembosia melastomatum* Mont. var. *microspora* Theiss., *Ann. Myc.* 11:438. 1913. On *Miconia*, Melastomataceae. Spores 22 x 11.5 μ . Syll. Fung. 24:494; *Ann. Myc.* 30:195. 1932.

39. *Lembosia memecyli* Syd., *Ann. Myc.* 29:246. 1931. *Morenoella memecyli* Syd., *Philipp. Jour. Sci.* 9:183. 1914. On *Memecylon*, Melastomataceae. Spores 20-23 x 8-10 μ .

40. *Lembosia portoricensis* Ryan, *Mycologia* 16:190. 1924. On *Coccoloba*, Polygonaceae. Ascomata 279-336 μ long, asci 34-39 x 19-24 μ , spores 17-24 x 7 μ .

41. *Lembosia warszewicziae* Henn., *Hedw.* 43:264. 1904. On

Warszewiczia, Orchidaceae. Ascomata 400-750 x 200-300 μ , asci 50-60 x 25-30 μ , spores 20-26 x 10-13 μ . Syll. Fung. 17:899.

42. *Lembosia parmularioides* Henn., Hedw. 43:265. 1904; Ule, Herb. Brasil. 2948, Berliner Mus.; Kew, Pasz. tab. 20, fig. 9-11. On Apocynaceae. Ascomata 250-300 μ , asci 60-80 x 20-24 μ . Doubtful species, the original description does not give hyphopodia. Ann. Myc. 11:449. 1913; Syll. Fung. 17:900.

43. *Lembosia nervisequa* Syd., Philipp. Jour. Sci. 9:183. 1914. On Litsea, Lauraceae. Ascomata 300-550 x 150-180 μ , asci 50-58 x 40-46 μ , spores 23-26 x 12-13 μ . Syll. Fung. 24:493.

44. *Lembosia melastomatum* Mont., Ann. Sci. Nat. ser. 4, 5:373. 1856. Ann. Myc. 11:438. 1913. *Lembosia diffusa* Wint., Hedw. 24:30. 1885. On Miconia, Melastomataceae; Posoqueria, Rubiaceae. Ascomata 700 x 250 μ , asci 70-96 x 42-52 μ , spores 35-40 x 16-20 μ . *Var. puttemansii* Arn. Ann. École Nat. Agr. Montp. 16:133. 1918. On Melastomataceae. Spores 27.5 x 13.5 μ . *Var. maublancii* Arn., Syll. Fung. 24:494. Ascomata and asci of *L. diffusa* are slightly smaller than those of *L. melastomataceae*. Syll. Fung. 2:742, 9:1106, 17:899; Mycologia 13:272. 1921; N. Y. Acad. Sci. 8:23. 1926; Rev. Myc. 7:1885; Ann. Myc. 28:385. 1930.

45. *Lembosia rolliniae* Rehm, in herb., Ann. Myc. 11:442. 1913. On Rollinia, Anonaceae; Tamonea, Verbenaceae; Miconia, Melastomataceae. Ascomata 0.3-0.35 x 0.1 mm., asci 50-60 x 30 μ , spores 24-26 x 10-11 μ . Syll. Fung. 24:491; N. Y. Acad. Sci. 8:23. 1926; Mycologia 16:190. 1924.

46. *Lembosia pandani* (Rostr.) Theiss., Ann. Myc. 11:457. 1913. *Asterina pandani* Rostr., Bot. Tid. 24:211. 1902. *Lembosia pandani* Rehm, Leaflet Philipp. Bot. 8:2932. 1916. On Pandanus, Pandanaceae. Ascomata 350-850 μ , asci 28-30 x 24-26 μ , spores 20-22 x 9-10 μ . Syll. Fung. 24:495; 17:881.

47. *Lembosia saccardoana* Sacc., Ann. Bot. 4:275, tab. 10, fig. 7. On Sansevieria, Liliaceae. Ascomata 150-200 μ , asci 70 x 42 μ , spores 28 x 14 μ . Syll. Fung. 22:563.

48. *Lembosia domingensis* Petr. and Cif., Ann. Myc. 28:385. 1930. On Exostema, Rubiaceae; Maytenus, Celatraceae. Ascomata 300-600 or 800 x 150-250 μ , asci 40-52 x 28-35 μ , spores 25-33 x 11-15 μ .

49. *Lembosia diplothemii* Henn., Hedw. 43:89. 1904. On Diplothemium, Palmae. Ascomata 100 μ long, asci 35 x 27 μ , spores 28-35 x 7-8 μ . Syll. Fung. 17:901.

50. *Lembosia cassupae* Henn., Hedw. 44:67. 1905. On Cassupa, Rubiaceae. Ascomata 450 x 250 or 600 x 300 or 1000 x 200 μ , asci 70 x 45-100 μ , spores 32-37 x 15-18 μ .

51. *Lembosia catervariae* Mont., Syll. Crypt. no. 651 and Guy no. 460. On Miconia, Melastomataceae. Ascomata 500-700 μ , asci 70-100 x 50-80 μ , spores 33-38 x 16-19 μ . Syll. Fung. 2:742; Ann. Myc. 11:428. 1913.

52. *Lembosia robinsonii* Syd., Philipp. Jour. Sci. 21:143. 1922. On *Eugenia*, Myrtaceae. Ascomata 300-500 or 1.25 mm. x 200-300 μ , asci 70-90 x 35-55 μ , spores 34-38 x 17-19 μ .

53. *Lembosia crustacea* (Cke.) Theiss., Ann. Myc. 11:432. 1913. *Asterina crustacea* Cke., Grev. 14:13. 1885. *Lembosia congregata* Syd., Ann. Myc. 8:40. 1910. *Lembosia breviuscula* (P. and S.) Syd., Syll. Fung. 17:899. *Lembosia diffusa* Wint. var. *breviuscula* P. and S., Malpighia 11:527. 1897. *Morenoella breviuscula* (P. and S.) v. Höhn., Frag. zur Myk. 10, no. 445. *Morenoella gedeana* Rac., Parasit. Algen und Pilz Javas 3:28. 1900. Syll. Fung. 14:654. 1899. On *Rhododendron*, Ericaceae. Asci 130 x 25 μ , spores 42-36 x 20-17 μ . Syll. Fung. 9:1106; 14:715; 16:654; 22:561; 9:380; Ann. Myc. 15:432. 1917; 28:246. 1930.

54. *Lembosia durbanana* van der Byl, So. Afr. Jour. Sci. 26:319. 1929. On *Chaetachma*, a lichen. Ascomata 200-340 x 140-120 μ , asci 24-54 x 18-24 μ , spores 16-26 x 6-8 μ .

55. *Lembosia sclerolobii* Henn., Hedw. 43:265. 1904. On *Sclerolobium*, Leguminosae; *Miconia*, Melastomataceae. Ascomata 500 x 180 μ , asci 60-70 x 40 μ , spores 25-28 x 9-11 μ . Syll. Fung. 17:899; N. Y. Acad. Sci. 8:1926; Mycologia 16:190. 1924.

56. *Lembosia pinorum* (Desm.) v. Höhn., Ber. Deutsch. Botan. Ges. 35:250. 1917. *Aulographum pinorum* Desm., Ann. Sci. Nat. ser. 2, 10:314; Duby Hyst. p. 37; De Notaris Pro. Ister. tab. 3, fig. 18. On *Pinus*, Pinaceae. Syll. Fung. 2:728. 1886.

56. MORENOELLA Spegazzini

Fungi Guar. I, Anal. Soc. Ci. Argentina 16:268. 1883.

Type: *M. ampulluligera* Speg.

Characters: Like *Lembosia* but paraphysate.

Literature: Ann. Myc. 11:425. 1913.

Synonymous genus: *Halbanina* Arn., Ann. École Nat. Agr. Montp. 16:163. 1918.

Arnaud states that *Halbanina* differs from *Halbania* "par les ascopores pourvues d'une seule cloison. Quelques caractères du type étant encore mal connus, ce genre est indique ici a titre provisoire." We consider it as *Morenoella*.

1. *Morenoella psychotriae* Ryan, Mycologia 16:194. 1924. Host unknown. Ascomata 84-120 x 192-276 μ , spores 2 x 9-10 μ .

2. *Morenoella cliftoniae* (Tracy and Earle) Theiss., Ann. Myc., 11:452. 1913. *Lembosia cliftoniae* Tracy and Earle, Bull. Torr. Bot. Club 22:208. 1896. On *Cliftonia*, Cryillaceae. Ascomata 100-150 x 40-70 μ , asci 20-25 x 10-15 μ , spores 9-11 x 4-5 μ . Syll. Fung. 14:713.

3. *Morenoella cestri* Ryan, Mycologia 16:192. 1924. Host unknown. Ascomata 302-448 x 56-89 μ , asci 12-26 x 5-12 μ , spores 9-12 x 3-5 μ .
4. *Morenoella ampulluligera* Speg., F. Guar. I, no. 303, Anal. Soc. Ci. Argentina, Buenos Aires 17:1883. *Lembosia ampulluligera* Speg., F. Puigg. no. 371, *ibid.* 17:1883. On Lauraceae. *Var.* meizospora Speg., F. Puigg. I, no. 371, *ibid.* 17:1883. Ascomata 150-200 x 100-120 μ , asci 30-35 x 15-18 μ , spores 12-13 x 5 μ . Syll. Fung. 9:1095. 1891.
5. *Morenoella fagraeae* Syd., Ann. Myc. 15:251. 1917. On Fagraea, Loganiaceae. Ascomata 400-800 x 100-150 μ , asci 28-35 x 13-16 μ , spores 12-14 x 4.5-5.5 μ . Syll. Fung. 24:501.
6. *Morenoella phillipsii* Doidge, Bothalia 1:205. 1927. On Ocotea, Lauraceae. Ascomata 240-600 x 90-160 μ , asci 26-33.5 x 18-20 μ , spores 13.5-15 x 5-6.3 μ .
7. *Morenoella oxyanthae* Doidge, Trans. Roy. Soc. So. Afr. 8:270. 1920. On Oxyanthus, Grumilea, Rubiaceae. Ascomata 400-600 x 250-300 μ , asci 23-30 x 13-16 x 3.5-5 μ .
8. *Morenoella calami* Rac., Parasit. Algen und Pilze Javas 3:28. 1900. On Calamus, Palmae; Epidendrum, Orchidaceae; Crescentia, Bignoniaceae. Ascomata 500-1500 x 120-150 μ , asci 40 x 14 μ , spores 16 x 6-7 μ . Syll. Fung. 16:654; Mycologia 16:192. 1924; N. Y. Acad. Sci. 8:23. 1926.
9. *Morenoella portoricensis* Speg., Bol. Acad. Nac. Ci. Cordoba 26:343. 1922. On Ocotea, Lauraceae. Ascomata 150-500 x 75-100 μ , asci 20-25 x 18-20 μ , spores 16-18 x 4-5.5 μ . Mycologia 16:193. 1924; N. Y. Acad. Sci. 8:24. 1926.
10. *Morenoella samarensis* Syd., Ann. Myc. 15:250. 1917. On Stephania, Memispermaceae. Ascomata 250-800 x 150-200 μ , asci 38-44 x 20-24 μ , spores 16-18 x 6-7 μ . Hyphopodia few, aparaphysate. Syll. Fung. 24:501.
11. *Morenoella* (?) *quercina* (Ell. and Mart.) Theiss., Ann. Myc. 11:448. 1913. *Aulographum quercinum* Ell. and Mart., Amer. Nat. 17:1283. 1883. Syll. Fung. 17:895. *Lembosia quercina* Tracy and Earle, Miss. Fungi p. 105, 1895. Syll. Fung. 14:714. On Quercus, Fagaceae. Ascomata 320 x 100 μ , asci 22 x 12-14 μ , spores 15-20 x 8 μ .
12. *Morenoella dothideoides* (Ell. and Ev.) v. Höhn., Frag. Myc. 8:357. 1909. *Maurothella* (?) *dothideoides* Arn., Ann. École Nat. Agr. Montp. 16:126. 1918. *Asteridium dothideoides* Ell. and Ev., Bull. Torr. Bot. Club 22:436. 1895. According to v. Höhnelt this is a typical *Morenoella*. An example at Cornell University (not the original) is a "Dothid" of the type *Polystomella*. Ann. Myc. 11:452. 1913. On Miconia, Melastomataceae; Andromeda, Ericaceae. Ascomata 300 μ in diameter or 500 x 200 μ , asci 30-40 x 18-21 μ , spores 20 x 7-8 μ . *Var.* *impetiolaris* Ryan, Mycologia 16:192. 1924. Syll. Fung. 14:700; N. Y. Acad. Sci. 8:24. 1926.

13. *Morenoella aniscocarpa* Syd., Ann. Myc. 12:559. 1914. On *Hopea*, Dipterocarpaceae. Ascomata at first round, 350-500 μ , later 500-1000 x 250-350 μ , asci 65-90 x 50-70 μ , spores 12-16 x 16-20 μ , hyphopodia nodulose. Syll. Fung. 24:499.

14. *Morenoella miconiae* Ryan, Mycologia 16:191. 1924. On *Miconia*, Melastomataceae. Ascomata 145-168 x 235-425 μ , asci 21-31 x 36-46 μ , spores 9-12 x 20-21 μ .

15. *Morenoella myrtacearum* (Speg.) Theiss., Ann. Myc. 11:430. 1913. *Lembosia myrtacearum* Speg., Fungi Puigg. no 374; Bol. Acad. Nac. Ci. Cordoba 11:577. 1889. Syll. Fung. 9:1095. 1891. *Morenoella mollinediae* Arn., Ann. École Nat. Agr. Montp. 16:137. 1918. On *Eugenia*, Myrtaceae; *Mollinedia*, Monimiaceae. Ascomata 400 x 100 or 700 μ long, asci 28-35 μ or 30-36 or 24 μ broad, spores 18-22 x 6-8 μ . Syll. Fung. 24:501; Ann. Myc. 11:1913.

16. *Morenoella laguensis* Syd., Ann. Myc. 12:560. 1914. On *Neolitsea*, Lauraceae. Ascomata 250-500 x 120-200 μ , asci 40-50 x 28-35 μ , spores 20-23 x 10-11 μ . Syll. Fung. 24:500.

17. *Morenoella decalvans* (Pat.) Theiss., Ann. Myc. 11:452. 1913. *Lembosia decalvans* Pat., Ann. Jard. Bot. Buitenzorg, p. 122. 1897. On *Pachygone*, Memispermaceae. Ascomata 160-300 x 100-150 μ , asci 40-50 x 23-28 μ , spores 20-23 x 8-10 μ . Syll. Fung. 14:712; Mycologia 16:192. 1924; N. Y. Acad. Sci. 8:24. 1926. *Var. langeriae* Ryan, Mycologia 16:193. 1924. On *Langeria*, Rubiaceae. Ascomata 190-257 x 316-347 μ , spores 21-24 x 5 μ . *Var. rondeletiae* Ryan, Mycologia 16:192. 1924. On *Rondeletia*, Rubiaceae. Ascomata 210-640 μ , long, asci 25-30 μ broad. *Var. stigmatophylli* Ryan, Mycologia 16:193. 1924. On *Stigmatophyllum*, Malpighiaceae.

18. *Morenoella langeriae* Ryan, Mycologia 16:192. 1924. On *Langeria*, Rubiaceae. Ascomata 414 x 68 μ , asci 43-48 x 36-41 μ , spores 24 x 12 μ .

19. *Morenoella whetzellii* Toro, Mycologia 17:134. 1925. On *Elsota*, Polygalaceae; *Securigera*, Leguminosae. Ascomata 150-350 x 124-140 μ , asci 39-45 x 27-31 μ , spores 21-24 x 7-9 μ . N. Y. Acad. Sci. 8:24. 1926.

20. *Morenoella tenuis* Syd., Ann. Myc. 12:560. 1914. On *Eugenia*, Myrtaceae. Ascomata 400-800 x 150-200 μ , asci 35-40 x 30-35 μ , spores 23-26 x 10-12 μ . Syll. Fung. 24:502.

21. *Morenoella pothoidei* (Rehm) Theiss., Ann. Myc. 11:442. 1913. *Lembosia pothoidei* Rehm, Philipp. Jour. Sci. 8:191. 1913. On *Pothoidium*, Araceae. Ascomata 400-500 x 300 μ , asci 80 x 40 μ , spores 25-27 x 12 μ . Syll. Fung. 24:491; Broteria 12:77. 1914. *Var. laevigatae* Ryan, Mycologia 16:193. 1924. On *Miconia*, Melastomataceae. Ascomata 336-493 x 145-201 μ , asci 53-73 x 36 μ , spores 24-29 x 12-14 μ .

22. *Morenoella puiggarii* (Speg.) Theiss., Ann. Myc. 11:442. 1913. *Lembosia puiggarii* Speg., F. Puigg. no. 375, Bol. Acad. Nac. Ci. Cordoba

11:578. 1889. On leaves. Ascomata 150-300 x 80-150 μ , asci 30-40 x 20-35 μ , spores 24-28 x 8-9 μ . Syll. Fung. 9:1106.

23. *Morenoella miconiicola* Ryan, Mycologia 16:191. 1924. On *Miconia*, Melastomataceae. Ascomata 331-448 x 470-860 μ , asci 33-43 x 69-84 μ , spores 12 x 24-29 μ .

24. *Morenoella melastomacearum* Ryan, Mycologia 16:194. 1924. On Melastomataceae. Ascomata 336-784 μ long, asci 41-48 x 55-72 μ , spores 12 x 26-29 μ .

25. *Morenoella giganteae* Ryan, Mycologia 16:194. 1924. On *Miconia*, Melastomataceae. Ascomata 784-1064 x 302-504 μ , asci 84-96 x 33-41 μ , spores 26-29 x 14 μ .

26. *Morenoella beilschmiediae* Yates, Philipp. Jour. Sci. 12:373. 1917. On *Beilschmiedia*, Lauraceae. Ascomata 400-600 x 100-150 μ , asci 36-45 x 25-30 μ , spores 25-30 x 6-7 μ . Syll. Fung. 24:500.

27. *Morenoella byroniae* (Arn.) Stev., n. comb. *Halbanina byroniae* Arn., Ann. Crypt. Exot. 4:91. 1931. On *Bryonia*, Cucurbitaceae. Spores 26-32 x 12-15 μ .

28. *Morenoella anisopterae* Syd., Ann. Myc. 12:560. 1914. On *Anisoptera*, Dipterocarpaceae. Ascomata 500-800 x 350-450 μ , asci 45-65 x 35-50 μ , spores 28-36 x 17-20 μ , hyphopodia nodulose. Syll. Fung. 24:499.

29. *Morenoella euopla* Syd., Ann. Myc. 26:97. 1928. On *Shorea*, Dipterocarpaceae. Ascomata 150-250 μ , asci 55-75 x 35-50 μ , spores 35-40 x 16-20 μ .

30. *Morenoella shoreae* Ryan, Mem. Dept. Agr. India 15:104. 1927. On *Shorea*, Dipterocarpaceae. Ascomata 247-544 x 330-346 μ , asci 48-52 x 40 μ , spores 36-40 x 20 μ .

31. *Morenoella erythrophlaei* (Henn.) Theiss., Ann. Myc. 11:446. 1913. *Lembosia erythroplaei* Henn., Engl. Bot. Jahrb. 38:117. 1905. On *Erythrophaleum*, Leguminosae. Ascomata 300-500 x 200-250 μ , asci 50-70 x 40-50 μ , spores 35-42 x 17-19 μ . Syll. Fung. 22:561.

32. *Morenoella bakeri* Syd., Ann. Myc. 15:250. 1917. On *Shorea*, Dipterocarpaceae. Ascomata 400-700 x 200-320 μ , asci 60-70 x 45-64 μ , spores 34-42 x 18-42 μ . Syll. Fung. 24:500.

33. *Morenoella macrospora* Sacc. and Paol., Myc. Malac., Atti R. Istit., Venet. Sci., Lett. ed Arti, 6 ser., 6:387. 1888. *Lembosia macrospora* Sacc. and Paol., Myc. Malac. *ibid.* On leaves. Ascomata 500-1000 μ long, asci 70 μ , spores 45 x 21 μ . Syll. Fung. 9:1096. 1891. Apparently the same fungus.

34. *Morenoella lophopetali* (Rehm) Theiss., Ann. Myc. 14:269. 1916. *Asterina lophopetali* Rehm, Leaflet Philipp. Bot. 6:2228. 1914. On *Lophopetalum*, Celastraceae. Ascomata 500 x 140-160 μ , asci 50-60 x 25-30 μ , spores 28-30 x 13-15 μ . Syll. Fung. 24:447.

57. ECHIDNODES Theissen and Sydow

Annales Mycologici 15:422. 1917.

Type: *E. lituræ* (Cke.) Theiss. and Syd.

Characters: Free mycelium, hymenium simple, ascomata linear, spores 2-celled, brown, non-hyphopodiate, paraphysate.

Literature: Ann. Myc. 11:436. 1913.

Synonymous genera: (1) *Maurodothella* Arn., Ann. École Nat. Agr. Montp. 16:123. 1918. Type: *M. psychotriæ* Arn., Ann. Crypt. Exot. 4:83. 1931. Syll. Fung. 24:497. This is very close to or identical with *Echidnodes*. (2) *Balansina* Arn., Ann. École Nat. Agr. Montp. 16:123. 1918. Type: *B. stellata* Arn., Syll. Fung. 24:477. 1926. This appears to be identical with *Echidnodes*.

1. *Echidnodes lituræ* (Cke.) Theiss. and Syd., l. c. *Lembosia lituræ* Sacc., Syll. Fung. 9:1106. *Aulographum lituræ* Cke., Grev. 12:38. 1883. On *Quercus*, Fagaceae. Ascomata 200-700 x 50-80 μ , asci 25-40 x 9-15 μ , spores 7.5 x 3.5 μ .

2. *Echidnodes asterinearum* Petr. and Cif., Ann. Myc. 28:381. 1930. On *Eugenia*, Myrtaceae; *Asterina*, a fungus. Ascomata 100-350 x 65-90 μ , asci 17-22 x 10-13 μ , spores 7-9 x 2.5-3 μ .

3. *Echidnodes microspora* (Chard.) Seaver and Chard., N. Y. Acad. Sci. 8:22. 1926. *Lembosia microspora* Chard., Mycol. 13:282. 1921. On *Ocotea*, Lauraceae. Ascomata 250-750 x 100-180 μ , asci 19-23 x 10-13 μ , spores 8-11 x 4-5 μ .

4. *Echidnodes cocoes* Syd., Ann. Myc. 26:135. 1928. On *Cocos*, Palmae. Ascomata 90-250 x 70-120 μ , asci 20-25 x 15-20 μ , spores 11-13 x 5-7 μ . Ann. Myc. 28:381. 1930.

5. *Echidnodes rhoïna* Doidge, Trans. Roy. Soc. So. Afr. 8:269. 1920. On *Rhus*, Anacardiaceae. Ascomata 300-500 x 90-150 μ , asci 35-40 x 20-24 μ , spores 13-16 μ .

6. *Echidnodes caespitosa* (Cke.) Theiss. and Syd., Ann. Myc. 15:422. 1917. *Ailographum caespitosa* Cke., Grev. 8:95. 1897. *Aulographum caespitosa* E. and E., Jour. Myc. 1:151. 1885. *Lembosia caespitosa* Sacc., Syll. Fung. 2:742. 1886. *Lembosia caespitosa* Sacc., Syll. Fung. 9:1107. 1891. On *Cypressus*, Pinaceae; on unidentified leaves. Ascomata 250-300 μ or 400 x 200-250 μ , asci 45-55 x 10-12 μ , spores 15-17 x 6 μ .

7. *Echidnodes heptapleuræ* (Sacc.) Theiss. and Syd., Ann. Myc. 15:422. 1917. *Lembosia heptapleuræ* Sacc., Bull. Orto. Bot. Nap. 6:52. 1921. On leaves. Ascomata 300-1000 x 100-120 μ , asci 40 x 12 μ , spores 16 x 5 μ . Syll. Fung. 24:492.

8. *Echidnodes pisoniæ* Stev. and Ryan, Bernice P. Bishop Mus. Bul. 19:76. 1925. *Maurodothella pisoniæ* Arn., Ann. Crypt. Exot. 4:85. 1931.

On *Pisonia*, Nyctaginaceae. Ascomata 120-125 x 200-500 μ , asci 20-21 x 43-50 μ , spores 7 x 15-18 μ .

9. *Echidnodes mammeae* Ryan, Mycologia 16:194. 1924. On *Mammea*, Guttiferae. Ascomata 123-145 x 168-280 μ , asci 17-21 x 24-41 μ , spores 7-10 x 18-19 μ .

10. *Echidnodes lirelliformis* (Cke.) Theiss. and Syd., Ann. Myc. 15:422. 1917. *Aulographum lirelliforme* Cke., Trans. Roy. Soc. Edinb. p. 393. 1887. *Lembosia lirelliformis* Sacc., Syll. Fung. 9:1108. 1891. On Wood. Ascomata 100 x 200 μ , asci 80 x 30 μ , spores 20 x 10 μ .

11. *Echidnodes stellata* (Arn.) Stev., n. comb. *Balansina stellata* Arn., Ann. École Nat. Agr. Montp. 16:123. 1924. On Myrsinaceae. Ascomata 500-1000 μ long, spores 20-20.5 x 9-10 μ .

12. *Echidnodes glonioides* (Rehm) Theiss. and Syd., Ann. Myc. 15:422. 1917. *Aulographum glonioides* Rehm, Hedw. 39:209. 1900. On Chevaliera, Bromeliaceae. Ascomata 500-1000 μ long, asci 50 x 25 μ , spores 15-18 x 6 or 22-25 x 9-10 μ . Syll. Fung. 16:659.

13. *Echidnodes festucae* (Lib.) Ryan, n. comb. *Lembosia festucae* v. Höhn., Ann. Myc. 15:366. 1917. *Aulographum festucae* Lib., Ard. no. 373, Duby Hyster. p. 38. On Festuca, Gramineae. Ascomata 200-800 x 40-80 μ , asci 18-22 x 8-11 μ , spores 8-9 x 2.5-3 μ , non-hyphopodiate.

14. *Echidnodes pachyasca* (Bres.) Theiss. and Syd., Ann. Myc. 15:422. 1917. *Lembosia pachyasca* Bres., Ann. Myc. 4:312. 1906. On Myrsine, Myrsinaceae. Ascomata 850 x 140 μ , asci 60 x 16 μ , spores 20-22 x 7-8 μ . Syll. Fung. 22:564; Ann. Myc. 11:425. 1913.

15. *Echidnodes xenospila* Syd., Philipp. Jour. Sci. 21:143. 1922. On Fagraea, Loganiaceae; Meliola, a fungus. Ascomata 350-450 x 120-180 μ , asci 35-45 x 30-35 μ , spores 22-25 x 9-10 μ .

16. *Echidnodes baccharidinicola* (Rehm) Theiss. and Syd., Ann. Myc. 15:422. 1917. *Lembosia baccharidinicola* Rehm, Ann. Myc. 11:445. 1913. *Lembosia drymidis* Lév., var. *baccharidinicola* Rehm, Ann. Myc. 5:532. 1907, *ibid.* 7:407. 1907. On Baccharis, Compositae. Ascomata 100-1500 μ long, asci 70-80 x 20-25 μ , spores 20-25 x 9-10 μ . Syll. Fung. 22:562.

17. *Echidnodes bromeliacearum* (Rehm) Theiss. and Syd., Ann. Myc. 15:422. 1917. *Lembosia bromeliacearum* Rehm, Hedw. 39:210. 1900. *Echidnodes bromeliac* Ryan, Mycol. 16:194. 1924. On Aregelia, Bromeliaceae. Ascomata 300 x 100 μ long, asci 40-25 x 30 μ , spores 18-22 x 6-7 μ . Var. *stellulata* (Rehm) Stev., n. comb. *Lembosia bromeliacearum* Rehm, var. *stellulata* Rehm, Pilze Sudamerika 8:210. 1900. *Aulographum maculare* B. and Br., var. *stellulata* Rehm, Hedw. 31:304. 1892. Pilze Sudamerika 5:297. 1898. On Arachnea, Euphorbiaceae, Ananas, Medularium, Guzmannia, Vriesea, Tillandsia, Bromeliaceae. Ann. École Nat. Montp. 16:130. 1918.

18. *Echidnodes hypophylla* (Syd.) Theiss. and Syd., Ann. Myc. 15:422. 1917. *Lembosia hyphophylla* Syd., Ann. Myc. 11:450. 1913. *Lembosia diffusa* Wint., var. *hyphophylla* Syd., Ann. Myc. 2:162. 1904. On Posoqueria, Rubiaceae. Ascomata 0.5 x 0.2 mm., asci 65-80 x 30-36 μ , spores 26-30 x 10-13 μ . Syll. Fung. 17:899; Ann. Myc. 11:452. 1913.

19. *Echidnodes psychotriae* (Arn.) Stev., n. comb. *Maurodothella psychotriae* Arn., Ann. École Nat. Agr. Montp. 16:124. 1918. On Psychotriae, Rubiaceae. Ascomata 0.65-0.9 mm. long, spores 30 x 14.5-15 μ .

20. *Echidnodes dendrochili* (Lév.) Theiss., Ann. Myc. 15:422. 1917. *Lembosia dendrochili* Lév., Ann. Sci. Nat. 3:59. 1845. Syll. Fung. 2:742. *Lembosia agaves* Earl, Mycologia 13:283. 1921. On Dendrochili, Orchidaceae; Agave, Amaryllidaceae. Ascomata 0.4-0.5 x 0.12-0.16 mm., asci 45 x 28 μ , spores 7-8 x 16-19 μ .

58. ECHIDNODELLA Theissen and Sydow

Annales Mycologici 15:422. 1917.

Type: *E. linearis* Syd.

Characters: Like *Echidnodes* but aparaphysate.

1. *Echidnodella rondeletiae* Ryan, Mycologia 16:195. 1924. On Rondeletia, Rubiaceae. Ascomata 228 x 72 μ , asci 27 x 12 μ , spores 7 x 2 μ .

2. *Echidnodella raillardiae* Stev. and Ryan, Bernice P. Bishop Mus. Bul. 19:76. 1925. On Raillardia, Compositae. Ascomata 63-72 μ long, spores 3.6 x 8 μ .

3. *Echidnodella myrciae* Ryan, Mycologia 16:195. 1924. On Myrcia, Myrtaceae. Ascomata 224-336 x 56-78 μ , asci 14-17 x 9-12 μ , spores 5 x 9 μ .

4. *Echidnodella angustiformis* (Tracy and Earle) Stev., n. comb. *Morenoella angustiformis* Theiss. Ann. Myc. 11:444. 1913. *Morenoella ilicis* Theiss., Ann. Myc. 11:451. 1913. *Lembosia angustiformis* Tracy and Earle, Bull. Torr. Bot. Club 22:208. 1896. *Lembosia ilicis* Tracy and Earle, *ibid.* On Ilex, Aquifoliaceae. Ascomata 120-250 x 50-80 μ , asci 16-22 x 10-13 μ , spores 8-10 x 4-5 μ . Syll. Fung. 14:713.

5. *Echidnodella linearis* (Syd.) Syd., Ann. Myc. 15:422. 1917. *Morenoella linearis* Syd., Ann. Myc. 1:250. 1903. On Cynomatra, Leguminosae. Ascomata 500-1500 x 100-150 μ , asci 30-35 x 14-16 μ , spores 11-13 x 3-4 μ . Syll. Fung. 24:498.

6. *Echidnodella hypolepidis* Doidge, Trans. Roy. Soc. So. Afr. 8:270. 1920. On Hypolepis, Cyperaceae. Ascomata 120-240 x 50-100 μ , asci 20-25 x 7-10 μ , spores 10-14 x 3.5-5 μ .

7. *Echidnodella prinoides* (Tracy and Earle) Theiss. and Syd., Ann.

Myc. 15:422. 1917. *Morenoella prinoides* Theiss., Ann. Myc. 11:451. 1913. *Lembosia prinoides* Tracy and Earle, Bull. Torr. Bot. Club 21:176. 1895. On *Ilex*, Aquifoliaceae. Ascomata 200-350 x 120-150 μ , asci 30-35 x 15-18 μ , spores 10-15 x 4-5 μ . Syll. Fung. 14:713.

8. *Echidnodella cavendishiae* Toro, Ann. Myc. 32:111. 1934. On *Cavendishia*, Vacciniaceae. Ascomata 513-618 x 125-171 μ , asci 34-48 x 16-20 μ , spores 13-15 x 6.8 μ .

9. *Echidnodella camphorae* (Earle) Theiss. and Syd., Ann. Myc. 15:422. 1917. *Morenoella camphorae* Theiss., Ann. Myc. 11:452. 1913. *Lembosia camphorae* Earle, Bull. Torr. Bot. Club 26:123. 1900. On *Camphora*, Lauraceae. Ascomata 500 x 100 μ , asci 25 x 20 μ , spores 18 x 6 μ . Syll. Fung. 16:663.

10. *Echidnodella fourcroyae* Ryan, Mycologia 16:195. 1924. On *Fourcroya*, Amaryllidaceae. Ascomata 112-168 x 324-336 μ , asci 24-28 x 33-36 μ , spores 9 x 17 μ .

11. *Echidnodella miconiae* Ryan, Mycologia 16:195. 1924. On *Miconia*, Melastomataceae. Ascomata 81-185 x 105-125 μ , asci 14-15 x 24-37 μ , spores 3-4 x 17-20 μ .

12. *Echidnodella rugispora* (Tracy and Earle) Theiss. and Syd., Ann. Myc. 15:422. 1917. *Morenoella rugispora* Theiss., Ann. Myc. 11:452. 1913. *Lembosia rugispora* Tracy and Earle, Bull. Torr. Bot. Club 22:208. 1896. On *Persea*, Lauraceae. Ascomata 400 x 100 μ , asci 30-45 x 7-8 μ , spores 15-20 x 8-10 μ . Syll. Fung. 14:712.

13. *Echidnodella cocculi* Stev. and Ryan, Bernice P. Bishop Mus. Bul. 19:76. 1925. *Maurodothella cocculi* (Stev. and Ryan) Arn., Ann. Crypt. Exot. 4:84. 1931. On *Cocculus*, Memispermaceae. Ascomata 500-650 x 200-284 μ , asci 14-18 x 36-41 μ , spores 21-23 x 7-9 μ .

14. *Echidnodella diaphana* Toro, Ann. Myc. 32:111. 1934. On *Conomorpha*, Myrsinaceae. Ascomata 239-371 x 137-171 μ , asci 38-45 x 31-34 μ , spores 20-22 x 9-12 μ .

15. *Echidnodella mabae* Stev. and Ryan, Bernice P. Bishop Mus. Bul. 19:76. 1925. *Lembosia mabae* (Stev. and Ryan) Arn., Ann. Crypt. Exot. 4:84. 1931. On *Maba*, Ebenaceae. Ascomata 397 x 227 μ , asci 54 x 33 μ , spores 21.6 x 7 μ .

16. *Echidnodella melastomacearum* Ryan, Mycologia 16:195. 1924. On *Miconia*, Melastomataceae. Ascomata 240-252 x 168-192 μ , asci 41-60 x 29-36 μ , spores 24-26 x 9 μ .

17. *Echidnodella marattiae* (Rac.) Theiss. and Syd., Ann. Myc. 15:422. 1917. *Morenoella marattiae* Rac., Parasit. Algen und Pilze Javas 2:19. 1900. On *Marattia*, Pteridophyta. Ascomata 0.3 mm. long, asci 36-40 x 20-22 μ , spores 26-28 x 5 μ . Syll. Fung. 16:654.

18. *Echidnodella ramosii* (Syd.) Stev., n. comb. *Morenoella ramosii*

Syd., Ann. Myc. 12:560. 1914. On *Pentacme*, Dipterocarpaceae. Ascomata 250-400 μ , asci 50-75 x 40-60 μ , spores 32-38 x 17-20 μ , paraphysate. Syll. Fung. 24:499.

19. *Echidnodella dipterocarpi* (Henn.) Theiss. and Syd., Ann. Myc. 15:422. 1917. *Morenoella dipterocarpi* Theiss., Ann. Myc. 11:457. 1913. *Lembosia dipterocarpi* Henn., Hedw. 47:261. 1907. On *Dipterocarpus*, Dipterocarpaceae. Ascomata 300-500 μ , asci 70-80 x 50-64 μ , spores 40-50 x 18-24 μ . Syll. Fung. 22:561.

20. *Echidnodella reticulata* (Starb.) Theiss. and Syd., Ann. Myc. 15:422. 1917. *Morenoella reticulata* Starb., Bih. K. Svensk. Vet.-Akad. Handl. 25:18. 1899. Afd. 3, no. 1, tab. 1, fig. 30. On *Vismia*, Guttiferaceae. Ascomata 250-400 x 75-100 μ , asci 46-50 x 40-44 μ , spores 30-32 x 18-19 μ . Syll. Fung. 16:653.

59. SYMPHASTER Theissen and Sydow

Annales Mycologici 13:217. 1915.

Type: *S. gesneraceae* (Henn.) Theiss. and Syd.

Characters: Free mycelium, hymenium simple, ascomata radiate, spores 2-celled, brown, paraphysate, non-hyphopodiate.

Literature: Ann. Myc. 15:418. 1917.

1. *Symphaster gesneraceae* (Henn.) Theiss. and Syd. *l. c.* *Cocconia gesneraceae* Henn., Hedw. 43:91. 1904. On leaves, Gesneraceae. Ascomata 1 mm. in diameter, asci 40-50 x 20-24 μ , spores 18-20 x 8-10 μ .

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LIST OF EXCLUDED SPECIES

(Numbers in parentheses refer to items in the bibliography)

Asterina

- agaves Ell. & Ev. (86), to
Perisporiaceae
aliena Ell. & Gallow (86)
alsophilae Dur. & Mont. (86), to
Polystomella
ammophilae Dur. & Mont. (86), to
Sphaerella
angraeci Roum. (86), to Asteroma—
immature
anomala Cke. & Harkn. (86),
immature
appendiculosa (M. & B.) Mont. (86),
to Dothidiaceae
asperata B. & C. (86), unripe
barleriae Pat. (86), to Perisporiaceae
bignoniae Ell. & Ev. (86), to
Perisporiaceae
cantareirensis Henn. (86), to
Dimeriella
capensis Kalch. & Cke. (86), to
Meliola
capnoides Ell. (86), to Asterella
carnea Ell. & Mart. (86), to Englerula
celastri E. & K. (86), to
Microthyriella
chamaenirii Rostr. (86), to Dimerina
cincta Berk. (86)
circinans B. & C. (86)
circularis Pat. (86), not Wint.
clavuligera Cke. (86), not
microthyriaceous
collinsii Schw. (80)
colubrina Ell. & Kelsey (86), to
Dictyopeltis
comata B. & Rav. (86), to
Polystomellaceae
concentrica Cke. (86), to Dothidiaceae
confluens Kalch. & Cke. (86), is only
a conidial stage
confluens Pat. (86), to Polystomella
conglobata B. & C. (86) (80), to
Otthiella
congregata B. & C. (86), to
Sphaeriaceae
connata B. & C. (86), to Otthia?
conspurcata Berk. (86), to
Brefeldiella
conyzae Pat. (86), to Dimeriella
cordobensis Speg. (86), to
Perisporiaceae
corollina Mont. (86), to Meliola
cuticulosa Cke. (86), to Microthyriella
decolorans B. & C. (86)
dichaenoides Cke. (86)
difformis Welw. & Curr. (86), to
Sphaeriaceae
diplodioides B. & C. (86)
discoidea Ell. & Mart. (86), to
Microthyriella

Asterina (*continued*)

- distincta Berk. (86)
ditricha Kalch. & Cke. (86)
dodonaei Pazz. (86), to Asterella
dubiosa Bomm. & Rouss. (86), to
Trichothyrium
epicera Berk. (86), a lichen
epilobii Desm. (86), to Venturia
erysiphoides B. & C. (86), to
Sphaerella
eucalypti (Pazz.) Sacc. (86), not
microthyriaceous
eucalypti Cke. & Mass. (86), to
Asteridium
eugeniae Mont. (86), to Dothidiella
examinans B. & C. (86), to
Montagmina
exasperans (Schw.) B. & C. (86)
filamentosa Pat. (86), to
Perisporiaceae
fragilissima Berk. (86), doubtful
fulginosa Pat. (86), to Dimerina
furcata Pat. (86), to Meliola and
Dimerina
furfuracea Ell. & Ev. (86)
gaultheria Curtis (86), to Epipeltis
globigera Ell. & Ev. (86), to
Englerula
goyazensis Henn. (86)
graminicola Ell. & Ev. (86), dubious—
to Asterella?
granulosa (Klotz) Hook. & Arn. (86)
grewiae Cke. (86), to Asterostomella
haemanthi Kalch. (86), to Cercospora
hederiae Desm. (86) (26), not a
fungus
hellibori Rehm (86), to Sphaeriaceae
himantia Sacc. (86), to Sphaerella
hystrix Pat. & Har. (86), to
Dimeriella
illicis Ell. (86), to Discomycetes
incompton Roberge (26)
infuscans Wint. (86), to Asterella
inquinans Ell. & Ev. (86), to
Ellisidothis
interrupta Wint. (86), to Entopeltis
intricata Ell. & Mart. (86), to
Microthyriella
irradians Pat. (86), to Epipolaenum
and Ellisidothis
irrepens (Schw.) Berk. (86), to
Meliola
juniperina Cke. (86), to Asteridium
karstenii Starb. (86), doubtful
labecula Mont. (86), to Trichopeltis
langolisi Ell. & Ev. (26), not
microthyriaceous
lata (Ayr.) Cke. (86), to
Melanconiaceae

Asterina (continued)

lepidigena Ell. & Mart. (86), to
Discomycetes
lepidigenoides Ell. & Ev. (26), to
Asteridium
lindigii Pat. (86), to *Dimerina*
lunariae Roum. (86), to *Sphaeriaceae*
mac-owaniana Kalch. & Cke. (86)
 (80), to *Parenglerula*
maesae Pat. (86), to *Perisporiaceae*
magnifica Syd. & Butl. (86), to
Trichopeltaceae
melaena (Fr.) Sacc. (86), to
Dothidiaceae
melioloides B. & Rav. (86) (80), to
Dimeriella
micropeltis B. & Br. (86)
micropeltis B. & C. (86), same as
micropeltoides
micropeltoides B. & C. (86)
microscopica Berk. (86), same as
Asterina stictica
microscopica Lév. (86), to *Sphaerella*
microsphaeroides Wint. (86)
microtheca Pat. (86) (80), to
Dimeriella
monotheca Pat. (86) (80), to
Balladyna
myriadea Cke. (86), to *Dimerium*
nimbosum Ell. & Mart. (80), not
radiate
nuda Peck. (61), to *Adelopus*
balsamicola and *Cryptopus nuda*
oleina Cke. (86), to *Zukalia*?
orbicularis B. & C. var. *interrupta*
 Thüm. (80)
oreophilum Speg. (80), not *radiate*
ostiolata B. & C. (86), unripe
palmarum (Kunze) Gaill. (86), to
Scolionema palmerum
palmicola Speg. (86), to *Auerswaldia*
parmlaria Henn. (86), to
Trichothyrium
pasaniae Henn. (86) (80), to
Trichothyrium
pauper Karst. & Roum. (86), to
Asterostomella
paupercula Ell. & Ev. (86), to
Asterella
pearsoni Ell. & Ev. (86), to *Asterella*
penicillata Pat. (86), to *Asterella*
peribebuyensis Speg. (86), to
Capnodiaceae
phaeostroma Cke. (86), to *Balladyna*
picea B. & C. (86) (80), to *Dimerium*
pinastri Sacc. & Ell. (86), to
Perisporiaceae
plantaginis Ell. (86), to
Mycosphaerella
pleurostylis B. & Br. (86), to *Meliola*
pseudocuticulosa Wint. (86), to
Microthyriella
purpurea Ell. & Ev. (86), to *Zukalia*
pyravanthae Desm. (86), to *Asteroma*

Asterina (continued)

quercigena (Berk.) Cke. (86), to
Trichothyrium
reptans B. & C. (86), to *Trichopeltis*
rhemii Henn. (86), not
microthyriaceous
rubi Niessel (86) (83), to *Asterella*
rubicola Ell. & Ev. (86), to
Sphaeriaceae
rufo-violescens Henn. (86), to
Trichothyrium
sabalicola Earle (86), dubious
scabiosae Richon (86), to *Asteridium*
schweinfurthii Henn. (86), to
Dothidiaceae
scutellifera Berk. (86), no perithecia
sepulta Berk. & Curt. (86), to
Dothidasteromella
setulosa Pat. (86), to *Meliola* and
Dimerium
silenes (Niessl) Sacc. (86)
solaris Kalch. & Cke. (86), to
Asterodothis
spartinae Ell. and Ev. (86)
sphaerelloides Ell. & Ev. (86), to
Dimerium
splendens Pat. (86), to *Piline*
splendens
spuria B. & C. (86), to *Capnodiaceae*
stictica Berk. (86)
stylospora Cke. (86)
subcuticulosa Cke. (86), to
Brefeldiella
subcyanea Ell. & Mart. (86) (83), to
Dictyothyrium
subfurcata Rehm. (86), to
Trichothyrium
tenuissima Patch (86), to
Chaetothyrium
toruligena Cke. (86), not
microthyriaceous
torulosa Berk. (86)
trichodea Rehm (86), to *Dimeriella*
tuberculata McAlp. (86) dubious
umbonata Desm. (80), to *Asteroma*
uvariae Lév. (86), to *Actinonema*
velutina B. & C. (86), to *Balladyna*
virescens Speg. (86), a lichen
vochysiae Henn. (86), to *Dimeriella*
xerophylli Ell. (86), to *Asteridium*
yoshinayae Henn. (86), to
Trichothyrium
yucatanensis Ell. & Ev. (86)
Asterinella
subcyanea Ell. & Mart. (83), to
Dictyothyrium
Aulographum
acicolum Harkn. (76) (85)
anaxaeum Sacc. & Sacc. (24), to
Hysterium
caespitosum Ell. & Ev. (76)
flicinum Lib. (24), to *Leptopeltis*
hieroglyphicum Rob. & Desm. (24),
 to *Asteroma*

Aulographum (continued)

- hysterioides* Sacc. & Syd. (76)
- ledi* Peck (76), to *Elsinoe*
- maculare* B. & Br. var. *dickiae* Rehm (25), to *Lembosiodothis*
- mugellianum* Paoli (24), to *Thyriopsis*
- reticulatum* Phill. & Harkn. (25), to *Schizothyrium*
- sarmentorum* Rehm (25), to *Rhabdostromemmina*

Calothyrium

- nubecula* (B. & C.) Theiss. (83)
- patagonicum* (Speg.) Theiss. (83), to *Hemisphaeriaceae*

Lembosia

- acicola* (Harkn.) Sacc. (85)
- albersii* Henn. (85), to *Asterodothis solaris*
- cocoës* Rehm (85), to *Hysteriales*
- compacta* Lévl. (85), to *Hysteriaceae*
- geographica* Mass. (85), to *Pseudolembosia*
- hysterioides* Sacc. & Syd. (85)
- javanica* (Pat.) Rac. (85), to *Parmularia*
- macula* Lévl. (85)
- nubecula* B. & C. (85)
- orbicularis* Wint. (85), to *Pseudolembosia*
- rhytismoides* (Schw.) B. & C. (85), to *Hysteriaceae*

Microthyrium

- abherrans* Speg. (83), to *Microthyriella*
- abnorme* Henn. (83), to *Dictyothyrium*
- acaciae* v. Höhn. (83)
- alsodeiae* Henn. (83), to *Micropeltis*
- anceps* Pазs. (83), dubious
- applanatum* Rehm (83), to *Microthyriella*
- carludovicae* Henn. (83), to *Metasphaeria*
- cetrariae* Bres. (26), to *Lichenopeltella*
- citri* Penz. (83), dubious
- coffae* Henn. (83), to *Microthyriella*
- consors* Rehm (83), to *Trichothyrium*
- crassum* Rehm (83), to *Polystomella*
- crustaceum* Pat. (83), to *Polystomella*
- disci* Rich. (83), to *Trichothyrium*
- elatum* Rehm (83), to *Clypeolum?*
- eucalypti* Henn. (83), to *Clypeolum*
- fuegianum* Speg. (83), to *Micropeltis*
- grammatophylli* Sacc. (83), to *Dothidiaceae*
- grandis* Niessl
- idaeum* Sacc. & R. (83), to *Melampsora*

Microthyrium (continued)

- lagunculariae* (Wint.) Rehm (83), to *Discomycetes*
 - lauraceae* Henn. (83), to *Micropeltis?*
 - laurantium* Henn. (83), to *Meliola*
 - lauri* v. Höhn. (83)
 - leopoldvilleanum* Henn. (83), to *Meliola*
 - longisporium* Pat. (83), to *Micropeltis?*
 - lunariae* (Kze.) Fekl. (83), to *Leptothyrium*
 - maculans* Zopf. (83)
 - madagascarensis* Karst. & Harkn. (83), sterile
 - mbdense* Henn. (83), to *Microthyriella*
 - melaleuca* Henn. (83), to *Dimerina*
 - microspermum* Speg. (83), to *Dimerina*
 - minutissimum* Thüm. (83), to *Entopeltis*
 - olivaceum* v. Höhn. (27) (83), to *Microthyriella*
 - pulchellum* Speg. (83), to *Polystomella*
 - rimulosum* Speg. (83), to *Microthyriella*
 - sebastinae* Theiss. (83), to *Microthyriella*
 - subcyanum* (Ell. & Mart.) Theiss. (83), to *Dictyothyrium*
 - urbani* Henn. (83), to *Microthyriella*
 - uvariae* Henn. (83), to *Microthyriella visci* Rich.
- Morenoella*
- discoidea* Rehm (85) (86), to *Discomycetes*
 - nephrodii* Rac. (85), to *Pseudolembosia*
- Myiocopron*
- coffeinum* (Ces.) Sacc. (85)
 - euryae* Rac. (84), to *Physalospora*
 - fecundum* Sacc. (84), to *Hemisphaeriaceae*
 - gironnierae* Harkn. & Karst. (84)
 - orbicular* (Cke.) Sacc. (84), to *Vizella?*
- Seynesia*
- araucariae* Rehm (83), not *microthyriaceous*
 - australis* Speg. (52), to *Asterostomella*
 - coccidea* Henn. (83)
 - elegantula* Syd. (83), to *Asterodothis*
 - grandis* (Niessl) Wint. (83), dubious
 - ilicina* Syd. (83)
 - minor* Ell. & Ev. (83), dubious
 - petiolocola* Henn. (83)

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 - Asterina punctiformis* var. *fimbriata*
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 - Asterina jacaratiae

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 - Prillieuxina intensa
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 - Morenoina lucens

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- Clypeolella leemingii

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- Parasterina dilleniae
- samarensis
- Dolicarpi
- Asterina orthosticha
- Tetracera
- Asterina tetracerae
- Halbaniella javanica

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- Asterina hians

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- Asterina anisopterae
- Morenoella anisopterae
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- Prillieuxina dipterocarpi
- Hopea
- Morenoella anisocarpa
- Parashorea
- Asterina caraminensis
- shoreana
- Pentacma
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- Shorea
- Asterina pluriporus
- Morenoella bakeri
- euopla
- shoreae
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- Euclea
- Seynesia orbiculata
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Elaeagnaceae

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- Elaeocarpus
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Ericaceae

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- Lembosiopsis andromedae
- Morenoella dothioides
- Phragmothyrium blyttii
- Gaulthera
- Seynesia costaricensis
- Gaylussacia
- Aulographum gaylussaciae
- Rhododendron
- Aulographum hederiae
- Lembosia crustacea
- Lembosina aulographoides
- Vaccinium
- Asterina tenella
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- Thyrosoma pulchellum

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- eupomatiae var. dalachampiae
- Parasterina melastomataceae
- Acalypha
- Asterina acalyphae
- tenuis
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- Asterina breyniae
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- Asterina ildefonsiae
- marginalis
- tenuis

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 - Asterina crotonicola*
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 - crotonis*
 - diplocarpa*
 - solanicola* var. *cristata*
- Dalachampia
 - Asterina eupomatiae* var. *dalachampiae*
 - tenuis*
- Drypetis
 - Asterina drypeticola*
 - drypetis*
- Exoecaria
 - Asterina exoecariae*
- Glochidion
 - Asterina cassiae*
 - lobulifera*
- Hevea
 - Lembosia glonioidea*
- Microdesmus
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- Ostodes
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- Ricinus
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 - Calothyrium pustulata*
 - stomatophorum*
 - Echidnodes lituræ*
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 - Phragmothyrium scheffleri*
- Azara
 - Asterina azarae*
- Casearia
 - Asterina juruana*
 - solanicola* var. *cristata*
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 - Asterina flacourtiæ*
 - spectabilis*

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 - Asterina celtidicola* var. *microspora*
 - Chaetothyriopsis panamensis*
- Scolopia
 - Asterina cylindrophora*
 - scolopiae*
 - Microthyrium ranulisporum*
- Trimeria
 - Asterina delicata*
- Xylosma
 - Asterina plectroniae*
 - Parasterina tonduzi*

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- Balladyna*
- Asterinella lembosioides*
- Meliola*
- Asterinella lembosioides*
- Echidnodes xenospila*
- Parodiopsis?*
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- Lembosia microtheca*

Gesneraceae

- Genus unknown
- Symphaster gesneraceae*
- Gesneria*
- Asterina dilabens*
- punctiformis*
- Mitraria*
- Asterina mitrariae*
- Rhytidophyllum*
- Asterina dilabens*
- Sarmienta*
- Asterina dilabens*
- Streptocarpus*
- Asterina streptocarpi*

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- Calothyriopeltis scaevolae*

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- Genus unknown
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 - Prillieuxina asterinoides*
- Andropogon*
- Aulographum culmigenum*
- Arundinaria*
- Aulographum arundinariae*
- Arundo*
- Asterina libertiae*
- Aulographum donacicola*
- Microthyrium mauritanicum*

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 - circinans
- Bromus
 - Aulographum bromi
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 - Microthyrium culmigenum
- Chusquea
 - Aulographum chusqueae
- Festuca
 - Calothyrium antarcticum
 - Echidnodes festucae
- Imperata
 - Aulographum maximum
 - Caenothyrium alang-alang
- Poa
 - Morenoina australis
- Penicellaria
 - Microthyrium senegalense
- Psamma
 - Microthyrium graminum
- Schizostachyum
 - Pycnoderma bambusinum
- Spartina
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 - Microthyrium calophylli
 - Lembosia sepotae
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 - Asterina solanicola var. cristata
 - Aulographum ciliatum
- Garcinia
 - Phragmothyrium garciniae
- Mammea
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 - ramonensis
 - stricta
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 - versipoda
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- Calothyrium subcolliculosum
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 - puiggarii
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 - macrospora
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- Prillieuxina lepidotricha
 - quinta
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 - circinans
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 - pachysperma
 - rimosa
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 - Prillieuxina humiriae

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 - Asterina mappiae
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 - Asterina escharoides
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- Lembosia luzulae
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- Asterina ildefonsiae
- Hyptis
- Asterina carbonaceae var.
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- Phyllostegia
- Asterina phyllostegiae
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- Genus unknown
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- Morenoella ampullifera var.
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- Nectandra
- Asterina ampullifera
- phoebes
- Morenoella ampullifera
- Neolitsea
- Asterina neolitseae
- Morenoella lagunensis
- Nothophoebes
- Polythyrium microchita
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- Echidnodes microspora
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- Lembosia microspora
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- portoricensis
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- Echidnodella rugispora
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- var. minor
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- Apuleia
- Seynesia apuleiae
- Caesalpinia
- Asterina ciferriana
- Myiocopron granulatum
- Phragmothyrium caesalpiniae
- Calliandra
- Asterinella brasiliensis
- Prillieuxina flexuosa
- Cassia
- Asterina elaeocarpi
- Castanospermum
- Parasterina platystoma
- Cynomatra
- Echidnodella linearis
- Cytisus
- Microthyrium cytisi
- Derris
- Asterina derridis
- singaporensis
- trachycarpa
- Asterinella gracilis
- Dipteryce
- Myiocopron cubense
- Erythrophaleum
- Morenoella erythrophylaei
- Herpetica
- Asterina elaeocarpi
- Holocalyx
- Parasterina holocalycis
- Hovea
- Asterina hoveaeifolia
- Inga
- Calothyrium ingae
- Thallochaete ingae
- Millettia
- Microthyrium millettieae
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- Myiocopron pereirae
- Pongamia
- Asterina derridis

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- Seynesia pulchella
- Sclerolobium
- Lembosia sclerolobii
- Securigera
- Morenoella whetzelli
- Sophora
- Lembosia graphioides var. sophorae
- Sweetia
- Parasterina bredmeyerae
- Zollernia
- Parasterina melastomataceae

Lichenes

- Cetraria
- Micropeltopsis cetraricola
- Microthyrium cetrariae
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- Lembosia durbana

Lilliaceae

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- Prillieuxina amboinensis
- Dracaena
- Lembosia patouillardii
- Sansevieria
- Lembosia saccardoana
- Smilax
- Peltella smilacis
- Platypeltella smilacis

Longaniaceae

- Chilianthus
- Asteromyxa inconspicua
- Fagraea
- Echidnodes xenophilae
- Morenoella fagraeae
- Strychnos
- Asterina strychni

Loranthaceae

- Genus unknown
- Asterina sphaerelloides
- Loranthus
- Asterina loranthicola
- Microthyrium loranthi
- Prillieuxina loranthi
- Phoradendron
- Asterinella phoradendri
- Prillieuxina phoradendri

Lythraceae

- Cuphea
- Asterina cupheae
- Lawsonia
- Asterina lawsoniae

Magnoliaceae

- Drymis
- Asterinella drymidis
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- olivascens
- scutellum

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- Illicium
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- Lembosia illiciicola
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- Phragmothyrium alabamensis

Malpighiaceae

- Genus unknown
- Asterinella multilobata
- Cirsosia manaosensis
- Phragmothyrium erysiphoides
- Banisteria
- Asterina banisteriae
- Brysonima
- Asterina brysonimae
- Asterinella uleama
- Heteropteris
- Asterina couepiae
- Hirea
- Asterinella leptotheca
- Malpighia
- Asterina indecora
- Stigmatophyllum
- Morenoella decalvans var. stigmatophylli

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- Asterina diplocarpa
- Malvastrum
- Asterina solanicola var. cristata
- Pavonia
- Asterina pavoniae
- solanicola var. cristata
- Sida
- Asterina diplocarpa

Marantaceae

- Genus unknown
- Lembosia microtheca
- Donax
- Aulographum donacis

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- Genus unknown
- Asterina pulla
- Asterinella puiggarii
- Lembosia melastomatum var. maublancii
- var. puttemansii
- Microthyrium melastomacearum
- Morenoella melastomacearum
- Parasterina hypophylla
- maublancii
- melastomaceae
- myiocoproides
- Prillieuxina melastomacearum
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- Asterina belluciae

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- Clidemia
 - Asterina schlechteriana
 - venezuelana
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 - Parasterina miconiae
- Conostegia
 - Asterina amadelpha
- Hirtella
 - Asterina inaequalis
- Memecylon
 - Asterina memecyloniae
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- Miconia
 - Asterina belluciaie
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- Aulographum culmigenum
- Echidnodella melastomacearum
- miconiae
- Lembosia catervaria
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- miconiicola
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- sclerolobii
- Morenoella dothideoides
- var. impetioilaris
- giganteae
- melastomacearum
- miconiae
- miconicola
- pothodei var. laevigatae
- Parasterina melastomataceae
- melastomatis
- miconiae
- transiens
- Prillieuxina antioquensis
- Tamonea
 - Asterina guianensis
- Tetrazygia
 - Asterina dilabens
 - tetrazygiae
- Tibouchina
 - Englera ulei
- Webera
 - Lembosia incisa

Meliaceae

- Genus unknown
- Asterina opposita
- Cipadessa
 - Parasterina cipadessae
- Dysoxylon
 - Asterinella dysoxyli
- Guarea

Meliaceae (continued)

- Asterina guaranitica
- Mallea
 - Asterina sphaerotherca
 - var. prodige
- Melia
 - Asterina sphaerotherca
 - var. prodige
- Trichilia
 - Asterina guaranitica
 - silvatica
 - trichiliae

Menispermaceae

- Anamirta
 - Prillieuxina anamirtae
- Cocculus
 - Echidnodella cocculi
- Pachygone
 - Morenoella decalvans
- Stephania
 - Morenoella samarensis

Monimiaceae

- Mollinedia
 - Lembosia brenesii
 - Morenoella myrtacearum

Moraceae

- Dorstenia
 - Asterina dorsteiniae
- Ficus
 - Seynesia ficina
- Maclura
 - Asterina balansae f. Maclurae
 - consociata
- Malaisia
 - Asterina malaisiae
- Taxotrophis
 - Stephanotherca micromera

Myrsinaceae

- Genus unknown
 - Echidnodes stellata
- Ardisia
 - Phragmothyrium fimbriatum
 - Pycnopeltis bakeri
- Myrsine
 - Calothyrium nebulosum
 - Echidnodes pachyasca
 - Phragmothyrium myrsines
- Rapanea
 - Asterina aphanes
 - Lembosia opaca
 - rapaneae
- Suttonia
 - Asterina suttoniae
 - Beelia suttoniae
 - Calothyrium suttoniae

Myrtaceae

- Genus unknown
 - Asterina balansae
 - Lembosia natalensis
 - Microthyriolum circinans

Myrtaceae (continued)

- Morenoina inaequalis
- Parasterina puttemansii
- Phragmothyrium manaosensis
- Seynesia olivascens
 - variolosa
- Calyptranthes
 - Asterinella caaguagensis
- Campomanesia
 - Asterinella caaguagensis
 - Aulographum myrtaceae
- Eucalyptus
 - Aulographum eucalypti
 - Lembosia eucalypti
 - Lembosiopsis eucalyptina
 - Microthyrium amygdalinum
 - eucalypticola
 - Seynesia microthyrioides
- Eugenia
 - Asterina assimilis
 - ditissima
 - fawcetti
 - myrciae
 - Caudella psidii
- Echidnodes asterianearum
 - Lembosia eugeniae
 - robinsonii
 - tenella
 - Microthyrium virescens
 - Morenoella myrtacearum
 - tenuis
 - Morenoina microscopica
 - Parasterina brachystoma
 - colliculosa
 - eugeniae
 - myrtacearum
 - pemphidioides
 - ramosii
 - Peltella valdivianum
 - Prillieuxina cylindrotheca
 - Seynesia chilensis
 - eugeniae
- Leptospermum
 - Microthyrium corynellum
- Metrosideros
 - Asterina rickii
 - Asterinella sublibera
 - Calothyriopeltis metrosideri
- Myrceugenia
 - Asterinella cupressina
 - Prillieuxina cylindrotheca
- Myrcia
 - Asterina myrciae
 - Asterinella uleana
 - Echidnodella myrciae
- Myrrhinium
 - Asterinella caaguazensis
 - puiggarii
 - Calothyrium confertum
- Myrti
 - Aulographum inconspicuum
- Psidium
 - Asterina crustacea
 - psidii
 - Caudella psidii

Myrtaceae (continued)

- Lembosia patouillardii
- Syzygium
 - Asterina quarta
- Temu
 - Campoa pulcherrima

Nyctaginaceae

- Pisonia
 - Echidnodes pisoniae
 - Prillieuxina intensa
- Ramisia
 - Prillieuxina amazonica

Ochnaceae

- Genus unknown
- Lembosiella polyspora

Oleaceae

- Olax
 - Asterina oligocarpa

Oleaceae

- Jasminium
 - Asterina lepiniana
 - spissa
 - Parasterina jasminicola
- Olea
 - Aulographum hederac
 - var. oleae
 - Lembosiopsis oleae
 - Morenoina graphioides
 - Phragmothyrium oleae
- Osmanthus
 - Calothyriella osmanthi
 - Calothyrium osmanthi
 - Prillieuxina intensa
- Phillyreae
 - Aulographum hederac

Onagraceae

- Epilobium
 - Aulographella epilobii

Opilliaceae

- Casjera
 - Asterina casjerac
 - echinospora
- Opilia
 - Asterina crebra

Orchidaceae

- Genus unknown
 - Scutellum javanicum
- Ansellia
 - Asterina raripoda
- Apostasia
 - Phragmothyrium schmidtiana
- Dendrochilus
 - Echidnodes dendrochili
- Epidendron
 - Asterinella epidendri
 - Morenoella calami
- Liparis
 - Asterina liparidis

Orchidaceae (continued)

- Oncidium
- Myiocopron corrientinum
- Stigmatostalycis
- Myiocopron stigmatostalycis
- Vanilla
- Lembosia rolfsii
- Warscewiczia
- Lembosia warscewicziae

Oxalidaceae

- Averrhoa
- Asterina venustula

Palmae

- Genus unknown
- Asterina subglobulifera
- transversalis
- Aulographum atro-maculans
- Myiocopron ciliatatum
- crustaceum
- palmarum
- Calamus
- Cirsosiella globulifera
- transversalis
- Lembosia microcarpa
- Morenoella calami
- Peltella conjuncta
- Prillieuxina calami
- Seynesia calamicola
- Yatesula calami
- Chamaedorea
- Lembosia poasensis
- Cocos
- Echidnodes cocoas
- Daemonorops
- Asterina bakeri
- Aulographum fimbriatum
- Cirsosiella transversalis
- Peltella conjuncta
- Diplothemium
- Lembosia diplothemii
- Elais
- Seynesia nobilis
- Pinanga
- Asterinella saginata
- Sabal
- Asterina sabalicola

Pandanaceae

- Freycinetia
- Myiocopron freycinetiae
- Seynesia atkinsonii
- Pandanus
- Aulographum intricatum
- pandani
- Lembosia pandani
- Myiocopron pandani

Passifloraceae

- Modecca
- (Adenia) Englera atrides
- Passiflora

Passifloraceae (continued)

- Asterina arnaudia
- azarea var. passiflorae
- megalospora
- var. meizopoda
- perconferta
- platasca
- Peltella bakerianum
- Tacsonia
- Asterina tacsoniae

Pinaceae

- Abies
- Microthyrium abietis
- Cupressus
- Asterinella cupressina
- Echidnodes caespitosa
- Juniperus
- Myiocopron baccarum
- Seynesia juniperi
- Pinus
- Aulographum pinorum
- Calothyriella pinophylla
- Calothyrium pinastri
- Kriegeriella mirabilis
- transiens
- Tsuga
- Microthyrium harrimani

Piperaceae

- Peperomia
- Calothyrium (?) bullatum
- Piper
- Asterina piperina

Pirolaceae

- Pyrola
- Phragmothyrium carniolica

Pittosporaceae

- Pittosporum
- Asterina densa
- effusa
- escharoides
- robusta

Polygalaceae

- Bredmeyera
- Parasterina bredmeyerae
- Elsota
- Morenoella whetzelii
- Securidaca
- Asterina pulchella

Polygonaceae

- Coccoloba
- Asterina coccolobae
- Lembosia tenella
- patouillardi
- portoricensis
- Lembosidium portoricense
- Seynesia coccolobae
- megalothecia

Proteaceae

- Cenarrhens
- Auglographum proteacium
- Grevillea
- Englera gymnosporiae
- Hakea
- Englerulaster baileyi
- Quadria
- Aulographum quadriae
- Roupala
- Ptychopeltis roupalae

Pteridophytes

- Genus unknown
- Aulographum tropicale
- Morenoina serpens
- Aspidium
- Asterina aspidii
- Cyathea
- Halbania cyathearum
- Dryopteris
- Morenoina africana
- Hymenophyllum
- Phragmothyrium hymenophylli
- Lycopodium
- Myiocopron lycopodii
- Marattia
- Echidnodella marattiae
- Phragmothyrium marrattiae
- Neprolepis
- Lembosia longissima
- Phegopteris
- Microthyrium phegopteridis
- Psilotum
- Peltella millepunctata
- Pteris
- Microthyrium litigiosum
- Trichomanis
- Phragmothyrium trichomanis

Rafflesiaceae

- Hypolepis
- Echidnodella hypolepidis

Rammirtaceae

- Raumirta
- Asterinella multilobata

Rapanaceae

- Genus unknown
- Seynesia santandariana

Rhamnaceae

- Rhamnus
- Asterina rhamnicola
- uncinata
- Trevoa
- Calothyrium jaffuelianum
- Zizyphus
- Asterina zizyphiae

Rosaceae

- Angelesia
- Asterina nodulifera

Rosaceae (continued)

- Banksia
- Prillieuxina systema-solare
- Chrysobalanus
- Asterina schroeteri
- Asterinella uleana
- Couepia
- Asterina couepiae
- Dryas
- Calothyrium dryadis
- Hirtella
- Phragmothyrium hirtellae
- Licania
- Asterina inaequalis
- schroeteri var. licaniae
- Photinia
- Aulographum hederace var. photiniae
- Potentilla
- Microthyrium arcticum
- Prunus
- Microthyrium epimyces
- Prillieuxina cryptocaryae
- Rubus
- Asterina balansae var. africana
- Aulographum confluens
- valdivianum
- Calothyrium versicolor

Rubiaceae

- Genus unknown
- Lembosia rubiacearum
- Alberta?
- Asterina gibbosa var. megathyria
- Basanacantha
- Asterina gibbosa
- Burchellia
- Prillieuxina burchelliae
- Canthium
- Parasterina canthii
- Cassupa
- Lembosia cassupae
- Coffea
- Microthyrium laurenti
- Phragmothyrium coffeicola
- Exostema
- Lembosia domingensis
- Genipa
- Asterina genipae
- Gonzalea
- Asterina ekmanii
- oligopoda
- Gouldia
- Asterina gouldiae
- Grumilea
- Morenoella oxyanthae
- Parasterina laxa
- Hillia
- Asterina dilabens
- Ixora
- Asterina ixorae
- Asterinella ixorae
- lugubris
- Prillieuxina distinguenda

Rubiaceae (continued)

- Krausia
 - Asterina radio-fissilis
- Langeria
 - Morenoella langeriae
 - decalvans var. langeriae
- Oxyanthus
 - Morenoella oxyanthae
 - Parasterina laxa
- Palicourea
 - Asterina erebia
- Pavetta
 - Asterina gibbosa var. megathyria
 - lipiniana
 - Lembosia pavettae
 - var. luzonensis
 - Microthyrium gomphisporum
- Plectronia
 - Asterina gibbosa var. megathyria
 - plectroniaecola
 - xylosmae
 - Asterinella lembosioides
 - palavanensis
 - Parasterina laxa
- Posoqueria
 - Echidnodes hypophylla
 - Lembosia melastomatum
- Psychotria
 - Asterina psychotriae
 - Calothyrium pasychothriae
 - ryani
 - Echidnodes psychotriae
 - Microthyrium psychotriae
- Randia
 - Asterina gibbosa var. megathyria
 - Lembosia philippinensis
- Rondeletia
 - Asterina advenula
 - Echidnodella rondeletiae
 - Morenoella decalvans var. rondeletiae
- Sickingia
 - Lembosia pittierii
- Tricalysia
 - Asterina gibbosa var. megathyria
 - Phragmothyrium distinctum
- Urophyllum
 - Asterina platypoda

Rutaceae

- Genus unknown
 - Microthyrium acervatum
- Aegle
 - Asterina delicatula
- Clausena
 - Asterina clausenicola
- Correa
 - Asterina correaecola
- Dictyoloma
 - Asterina dictyolomatis
- Fagara
 - Parasterina fagarae
- Glycosmis
 - Asterina banguiensis

Rutaceae (continued)

- Pilocarpus
 - Scutellum guaraniticum
- Rhabdodendron
 - Parasterina rhabdodendri
- Xanthoxylum
 - Seynesia olivascens

Sabiaceae

- Champereia
 - Asterina decipiens
 - elmeri
- Meliosma
 - Asterina meliosmaticola
- Osyridicarpus
 - Asterina polythryria
- Santalum
 - Asterina congesta

Sapindaceae

- Genus unknown
 - Asterina carbonacea var. huallagensis
 - Microthyrium paraguayense
- Guioa
 - Lembosia inconspicua
- Mischocarpus
 - Microthyrium mischocarpi
- Paullinia
 - Prillieuxina multilobata
- Schmidelia
 - Asterina guaranítica

Sapotaceae

- Genus unknown
 - Asterina paraguayensis
- Calophyllum
 - Lembosia sepotae
 - Microthyrium calophylli
- Chrysophyllum
 - Asterina carbonacea var. acanthopoda
 - chrysophylli
 - opaca
 - sydowiana
- Dipholis
 - Asterina dipholdis
- Micropholis
 - Asterina sydowiana
- Mimusops
 - Prillieuxina minusopsidis
- Sideroxylon
 - Asterina diaphorella
 - laxiuscula
 - Parasterina implicata
 - sacardoana

Saxifragaceae

- Genus unknown
 - Clypeolla stellata
- Escallonia
 - Asterina negeriana
- Polyosma
 - Parasterina melanotes

Scrophylariaceae

- Ildefonsia
 - Asterina balansae
 - ildefonsiae
- Veronica
 - Asterina veronicae

Simarubaceae

- Picrasma
 - Asterina lobata
 - Polythyrium costaricense

Solonaceae

- Genus unknown
 - Microthyriolum oligosporum
- Acnistus
 - Calopeltis acnisti
- Cestrum
 - Asterina coriacea
 - diplocarpa var. cesticola
 - solanicola var. cristata
 - vagans var. subreticulata
 - Asterinella leptotheca
 - Aulographum cestri
- Jochroma
 - Seynesia iochromatis
- Solanum
 - Asterina balansae f. solani
 - verbascifolii
 - f. solani
 - benguensis
 - consobrina
 - dilabens
 - diplopoda
 - effusa
 - henningsii
 - portoricensis
 - solanicola var. cristata
 - solanicoloides
 - vagans
 - var. subreticulata
 - Asterinella brasiliensis
 - leptotheca
 - Calothyrium leptosporum
 - Clypeolella solani
 - Prillieuxina diaphana

Sterculiaceae

- Büttneria
 - Asterina büttneriae
- Cola
 - Parasterina africana
- Helicteres
 - Asterina leptalea
- Lasiopetalum
 - Actinomyxa australiensis

Styracaceae

- Styrax
 - Asterina dispar
 - guaranitica
 - styracina
 - Asterinella uleana
 - Microthyrium styracis

Styracaceae (continued)

- Parasterina brachystoma
- Trichasterina styracis

Symplocaceae

- Genus unknown
 - Prillieuxina cryptocaryae
- Symplocus
 - Asterina grammocarpa
 - indica
 - sodalis
 - Calopeltis tetraspora

Taxaceae

- Dacrydium
 - Microthyrium microscopicum

Theaceae

- Camellia
 - Asterina camelliae
- Eurya
 - Aulographum euryae

Thymelaceae

- Daphne
 - Seynesia pontica
- Phaleria
 - Asterina bataanensis

Tilliaceae

- Corchorus
 - Asterina diplocarpa
- Tilia
 - Lembosina copromya
- Triumfetta
 - Asterina isothea
 - triumfettae

Turneraceae

- Turnera
 - Asterina solanicola var. cristata

Ulmaceae

- Celtis
 - Asterina celtidicola
- Sponia
 - Asterina sponiae
- Trema
 - Asterina sponiae

Umbelliferae

- Angelica
 - Asterina pittieri
 - Microthyrium angelicae
- Foeniculum
 - Peltella argentinense

Urticaceae

- Leucosyke
 - Asterina phaleriae
 - Prillieuxina capizensis
 - microspila
- Phenax
 - Asterina phenacis
- Pipturus
 - Asterina pipturi

Vacciniaceae

- Cavendishia
- Echidnodella cavendishiae

Verbenaceae

- Gmelia
- Asterinella gmelinae
- Premna
- Asterina pusilla
- Asterinella creberima
- Tamonea
- Lembosia rollinae
- Vitex
- Asterina sphaerotherca
- var. prodige

Violaceae

- Alsodeia
- Seynesia melanosticta
- Rinorea
- Asterina vagans var. subreticulata
- Viola
- Asterina undulata
- violae

Vitaceae

- Cissus
- Parasterina spinosa
- Leea
- Calothyrium aphanellum

Zingiberaceae

- Alpenia
- Peltella smilacis

ALPHABETICAL LIST OF SPECIFIC NAMES

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**THE BRANCHIOBDELLIDAE
(OLIGOCHAETA)
OF NORTH AMERICAN
CRAYFISHES**

WITH THREE PLATES

**BY
CLARENCE JAMES GOODNIGHT**

**CONTRIBUTION FROM THE ZOOLOGICAL LABORATORY OF THE
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I. INTRODUCTION

THE BRANCHIOBELLELLIDAE comprise a family of annelid worms which live on the bodies of crayfish. In the older literature this family has been designated as the Discodrilidae, but Hall (1914) showed this name to be untenable as there is no genus Discodrilus. This family is known from Europe, eastern Asia and Japan, and North and South America. So far as is known, these worms are always found on crayfish, but the question whether or not they are parasitic in their food habits is far from settled. The writer believes and will attempt to show that their food consists largely of diatoms and that they are for the most part non-parasitic.

The descriptions of the American branchiobdellids are scattered throughout a number of papers published in various sources, some of which are not generally available. The last paper dealing with the taxonomy of the American forms (Ellis, 1919) appeared twenty years ago. In no recent paper has there been any attempt at synthesis of all the described species by means of diagnostic keys. The last attempt at such synthesis was by Hall in 1914, but his material was so meager that his keys are inadequate, and over half the species now known were described after his paper was published. Except for a new species, inadequately described from poorly preserved material, he included no specific descriptions or comparisons.

Of the known species the locality records are from only a few well-known areas, and many are known from the type locality only. Thus the geographical limits of the species are poorly defined. The last important paper was by Ellis in 1919. He described in fine detail a number of new species and gave new locality records for a few old ones, but he presented few diagnostic keys and attempted very little synthesis.

The present study summarizes the existing information on American forms, presents diagnostic keys, further defines the range of the species, and adds four new forms which were encountered. In an attempt to evaluate the taxonomic importance of morphological characters, the family is divided into two natural groups, the forms with two pairs of testes being recognized as the basis for a new subfamily (Cambarincolinae). The present study also adds to the existing knowledge of the biology of the family.

II. ACKNOWLEDGMENTS

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entire period of study Professor Van Cleave has given helpful advice and encouragement, thus contributing largely to whatever success this investigation has attained.

The writer is indebted to Dr. Carl L. Hubbs for permission to examine the material in the Museum of Zoology, University of Michigan, and for a place to work while at the museum. He also wishes to express his thanks to Dr. David H. Thompson for permission to examine the material in the collections of the Illinois State Natural History Survey, to Dr. Percy Moore for advice and criticism, to Dr. A. S. Pearse for material from North Carolina, to Dr. John D. Mizelle for specimens from Oklahoma, to Dr. James Sanders for specimens from South Dakota, to Dr. J. Henry Walker for material from Alabama and Florida, and to Dr. Edwin P. Creaser for information concerning the location of collections.

The writer is likewise indebted to his fellow graduate students, especially Dr. Harry G. Kimpel, for assistance in making field collections.

III. MATERIALS AND METHODS OF STUDY

LARGE AMOUNTS of material were available for this study. In general, two methods were employed to obtain this material: (1) actual collecting of crayfish and removing of worms, and (2) examining museum jars of preserved crayfish and obtaining the worms that had fallen to the bottom or still remained on the dead crayfish.

For fixing the worms, the best results were obtained with warm A.F.A. (85 parts 85% alcohol, 10 parts formalin, 5 parts glacial acetic acid). The crayfish were dropped into this solution and the fixed worms were gathered from the bottom after decanting. However, the worms fixed in formalin and higher grades of alcohol were found to be adequate for taxonomic studies, though slightly contracted. Worms were studied both from total mounts and from sectioned material. The best results with total mounts were obtained by running the worms up through the grades of alcohol and clearing in xylol, then mounting in balsam without staining. In some cases excellent results were also obtained by staining with a solution of four drops of Delafield's hematoxylin and four drops of Ehrlich's acid hematoxylin in 20 cc. of a saturated water solution of potassium alum, then destaining, neutralizing in running tap water, clearing, and mounting in balsam. Borax carmine was also used with some success.

While in most cases the significant taxonomic details could be demonstrated in total mounts by means of dorsal, ventral, and lateral views, these findings were checked by means of sections cut at 10 or 20 microns. Transverse, frontal, and longitudinal series were prepared.

Excellent results were obtained by staining the sections with Delafield's hematoxylin, going up through alcohols to 70%, destaining in acid 70%, running down to water, and washing in tap water 30 minutes or longer, going up to 95% alcohol, counterstaining with eosin, clearing, and mounting in balsam. Heidenhain's iron hematoxylin, with eosin as a counterstain, was used to some extent.

The paraffin ribbon was affixed to the slide with bakelite. A mixture of 2.0 grams gelatin, 1.0 grams phenol, 15 cc. glycerin, and 100 cc. distilled water was smeared on the slide, and the sections were floated on with 4% formaldehyde solution.

Of the twenty-two species included in this study, all but three have been studied from large amounts of material, many species being represented by hundreds of specimens.

Field observations were also carried on during this study to determine the abundance and distribution of the branchiobdellids.

IV. HISTORY OF INVESTIGATIONS ON THE BRANCHIOBDELLIDAE

APPARENTLY the first published note of this group was by Rosell (1755). Braun in 1805 mentioned them in a description of some leeches. A few other papers, Müller (1806) and Savigny (1809), mention them also, but it was not until 1823 that the first taxonomic description was given. In that year Odier published in the *Mémoires de la Société d'Histoire Naturelle de Paris* a very fine description of the common branchiobdellid of western Europe which he called *Branchiobdella Astaci*. He believed it was a leech and closely related to the genus *Hirudo*. He gives (p. 75) the following characterization of the genus: "un corp contractile un peu aplati, composé de dix-sept anneaux, terminé par un disque préhensile; une tête oblongue, garnie de deux lèvres; une bouche armée de deux mâchoues cornées, triangulaires, dont la supérieure plus grande, et point d'yeux." He spends some time (p. 76) pointing out that this form was a leech and not a tipulid larva as one M. de Blainville had previously reported to the society.

Apparently no important work was published on the group for the next twenty years. Then in 1835 G. Henle reported a careful anatomical study in an article entitled "Ueber die Gattung *Branchiobdella*." Vallot in two papers (1839 and 1845) also reported briefly on this group. Moquin-Tandon in his leech monograph of 1846 included a description of *Branchiobdella*.

Previous to 1851 all work on this family was by Europeans and on European species, but in that year Joseph Leidy published in the *Proceedings of the Academy of Natural Sciences of Philadelphia* (p. 209) a

description of an American species which he called *Astacobdella philadelphia*. There followed a series of brief papers by Europeans on branchiobdellid anatomy, but thirty-one years elapsed before the next significant taxonomic paper was published.

The next American paper was by Verrill (1873). In his synopsis of American leeches he republished Leidy's description of 1851.

A series of papers published in Europe on European species next appeared. Whitman (1882) published a description of *Branchiobdella pentadonta*, a new species. Next appeared a number of papers on the anatomy and development of Branchiobdella. These were by various Europeans who were only incidentally interested in the group. These included Gruber, Lemoine, Voigt, Ostroumoff, Vejdowski, Rohde, Salensky, and others.

In 1894, forty-three years after Leidy's paper, Moore published descriptions of "Some Leech-like Parasites of American Crayfish." He included *Branchiobdella illuminata*, *B. pulcherrima*, *B. instabilis* new species, and *B. philadelphia* (Leidy) in his discussion. The following year, in another paper, he described a new genus, Pterodrilus, which included two new species, *P. alcornis* and *P. distichus*. In 1895 Moore published a very fine account of the anatomy of *Bdellodrilus illuminatus* (Moore). This is the best general anatomical account yet published and the only one on an American species. He pointed out in this paper the need for more work on the nephridial system. This complicated system was worked out and the results were published the following year by Voinow on *Branchiobdella varians*. Moore in 1897 gave an excellent account of the nephridial system of *Bdellodrilus illuminatus*. Four years later, 1901, his monograph on the leeches of Illinois was published in which he mentioned the fact that in the collection *Bdellodrilus philadelphia* was found on *Cambarus diogenes* and *C. blandingi*. This paper marks the end of Moore's work on Branchiobdellidae. Afterwards he turned his attention largely to leeches.

F. Schmidt pointed out in his papers (1902 and 1903) that the musculature was more definitely similar to the Oligochaeta than to the Hirudinea. Some time later (1905) Pierantoni, an Italian, began to publish on the group, giving a description of *Cirrodrilus cirratus*, a new species from Japan. He followed this in 1906 by a brief general account of the genus Branchiobdella. In another paper (1906b) he described two new forms, *Branchiobdella tetradonta* from California and *B. digitata* from Japan. In the same year Smallwood, an American, gave an account of some observations on the life habits of some branchiobdellids in the neighborhood of Clear Lake, New York.

The year 1912 is a memorable one in the study of this group, for

in that year Pierantoni published the first monograph.¹ In this he summarized the anatomy of branchiobdellids and showed that they are definitely Oligochaeta. He included several new species and all previous ones. He listed: *Cirrodriulus cirratus* Pier. from Japan, *Branchiobdella parasita* Henle, *B. pentadonta* Whitman, *B. hexadonta* Gruber, and *B. astaci* Odier from Europe; *B. minuta* n. sp. from Amur-Riff; *B. anatis* n. sp. and *B. dubia* n. sp. of unknown habitat; *Stephenodriulus sapporensis* Pier., *S. japonicus* n. sp. from Japan; *S. koreanus* n. sp. from Korea. From America he listed *Branchiobdella tetradonta* Pier., *B. americana* n. sp., *Bdellodriulus pulcherrimus* (Moore), *B. instabilis* (Moore), *B. illuminatus* (Moore), *B. philadelphicus* (Leidy), *Pterodriulus alcicornus* Moore, and *P. distichus* Moore.

In the same year (1912) Ellis described a new American worm, *Cambarincola macrodonta* from Colorado. He included a brief key to some of the described forms. Two years later (1914) Hall briefly and inadequately described a new species from Utah which he called *Ceratodriulus thysanosomus*. He also included a summary of locality records for American species and erected the superfamily Branchiobdelloidea. In 1915 Tannreuther published a cell lineage study using *Cambarincola philadelphica* as a subject. In 1918 Frank Smith included a few species in his chapter in Ward and Whipple's "Fresh Water Biology." In the same year Ellis listed species he collected around Douglas Lake, Michigan. In 1919 he published an account of "The Branchiobdellid Worms in the Collection of the United States National Museum." He described as new *Xironodriulus formosus*, *Xironogiton occidentalis*, *Xironogiton oregonensis*, *Pterodriulus mexicanus*, *Pterodriulus durbini*, *Cambarincola vitrea*, *Cambarincola chirocephala*, and *Cambarincola inversa*. This is the best single article on the taxonomy of the American species, but no generic keys and few specific keys are included. This was Ellis' last paper on the branchiobdellids. In 1928 Alessandra gave an account of a new European species, *Branchiobdella italica*.

Stephenson published a monograph on the Oligochaeta in 1930, in which he gave a lengthy discussion of the Branchiobdellidae, including as valid genera: Branchiobdella, Cirrodriulus, Stephanodriulus, Bdellodriulus, Pterodriulus, Ceratodriulus, Cambarincola, Xironodriulus, and Xironogiton. In 1932 H. Yamaguchi began writing on this group. He published several preliminary papers and finally in 1934 a monograph of the Japanese forms including nineteen species in three genera. In 1935 Evans collected worms in Champaign County, Illinois. He reported (1939) four species: *Cambarincola macrodonta*, *C. vitrea*, *C. chirocephala*, and *Bdellodriulus illuminatus*.

V. MORPHOLOGY OF THE BRANCHIOBELLELLIDAE

PIERANTONI (1912) in the first general monograph of the group characterizes the Branchiobdellidae as follows:

Corpo diviso in due regioni, una cefalica di tre segmenti con lobo preorale ventosiforme, bilobo o plurilobato, con o senza appendici digitiformi ed un'altra regione, del tronco, di 11 segmenti, terminata da ventosa e priva di setole.

Bocca provvista di due forti mascelle più o meno dentate.

Sistema circolatorio fatto da un vaso dorsale con seno perienterico e da un vaso ventral riunito a quello da quattro paia di tronchi trasversali anteriori e da uno posteriore.

Sistema escretore fatto da due paia di nefridii posti nei segmenti del tronco apertisi per pori dorsali posti nel 4° e nel 9° segmento del tronco.

Testicoli 1 o 2 paia, nel 5° e nel 6° segmento del tronco.

Spermateca nel 5° segmento, impari; atrio ugualmente impari provvisto di pene e di condotti seminali pari in numero di due o di quattro, con corrispondenti paia di imbuti ciliati nel seg. 5° e nel 6°, trattenuti dai sepimenti posteriori corrispondenti; ovarii e pori femminili nel 7° segmento.

A. EXTERNAL CHARACTERS

The branchiobdellids are a homogeneous group of worms ranging from 1 to 12 mm. in length. The body consists of two parts, the head and the trunk. A caudal sucker is present at the posterior end of the body.

The head is somewhat cylinder-shaped. The mouth is surrounded by fleshy lips, which may or may not be lobed. In some forms the lobes may be extended into tentacles. Inside the mouth, at the base of the muscular ring or sucker, is a circlet of numerous minute papillae. The head shows a groove at the base of the lips and a median dorsal depression. The lack of definite segmentation has led to various interpretations of the number of annuli included. Pierantoni (1912) considered that the head consists of a prostomium and three segments; the prostomium represented by the peribuccal region, the first cephalic segment between the peribuccal ring and the dorsal pit, the second segment posterior to the pit, and the third, indistinct in most species, bordering the trunk region. According to Pierantoni there are three bilobed ganglia and three vascular commissures connecting dorsal and ventral vessels; so he concluded that the internal anatomy agreed with his three-segment theory. Moore (1895b:499) considered the peribuccal ring as a segment and so believed there are four head segments. Schmidt (1905) agreed with Pierantoni that there are only three, while Vejdowski (1884:39) thought that there are six or seven segments, since the ganglia are bilobed. Ellis (1912:482) and Stephenson (1930:796) agree with Moore. Stephenson (1930:796-797) summarizes the evidence for the four-segment head theory as follows:

It would, however, seem to be erroneous to describe the circumbuccal ring as a prostomium; it is obviously a peristomium, and the peristomium is universally the first true segment in the Oligochaeta. If so reckoned here, there would be

four segments in the head, the prostomium having disappeared (as, e.g., in *Chaetogaster*) as a distinct division. Moreover, in the Limicolae the first segment has no vascular commissures (apart from the arch uniting the anterior ends of the dorsal and ventral vessels); the first of the commissural vessels is in segment II. The vascular arrangement of the Branchiobdellidae, therefore, also indicates four segments to the head. Again F. Schmidt (1905) describes a thickening situated at the middle of the length of the pharyngeal connective on each side, which is due to an aggregation of nerve cells; a nerve is given off from the connective just above, and another from just below, this thickening, and these nerves pass forward to the buccal segment. The thickening is in addition to the buccal ganglion (with a visceral distribution), and seems to represent the proper ganglion of the buccal segment, so that again four cephalic segments seem to be indicated. Lastly, by counting four head segments the position of the genital apertures and organs is brought into line with that in the majority of genera of Lumbriculidae, with which the Branchiobdellidae are closely allied.

My own observations tend to support the four-segment theory.

The trunk region is variously shaped in different species. In some forms, as *Cambarincola*, it is cylindrical and relatively uniform in diameter throughout its entire length. In others as *Xironodrilus*, it is flattened and wider in segments VI and VII than in the others. *Xironogiton* is flattened and widest in the posterior segments.

Dorsal appendages are present in some forms. In *Pterodrilus* these consist of cylindrical fleshy protruberances along the median dorsal line of the body. In *Cirrodrilus* they extend transversely across the dorsal surface as a pointed band with usually six, sometimes seven or eight, points on the free margin. These dorsal appendages usually have ridges of transverse muscle fibers associated with them. Little is known of their function. Moore (1895a:450) first pointed them out on American species. He says:

Regarding the function of the dorsal organs there is little to say. A priori one would expect them to be respiratory, but the apparent entire absence of blood vessels, which are unrevealed after a careful study of sections would tend to throw strong doubt upon such an interpretation. Irregular spaces are evident here and there between the muscle fibres but these appear to be continuous with the inter-muscular spaces which are developed between the circular and longitudinal muscle fibres of the body walls, and have not been traced into any communication with the body cavity. Until an opportunity is afforded of studying living examples in their proper habitat, and observing the uses to which these organs are put, no opinion can be vouchsafed.

Externally the trunk consists of eleven segments. The first eight are quite distinct and prominent. They are divided into two unequal parts by a sulcus towards the posterior fourth of the segment. The last three segments are smaller and less distinct. The last segments form the caudal sucker, the principal attachment organ of the worm. On a few species additional small, somewhat concave, glandular adhesive disks are present near the lateral margin of segments VIII and IX. This is true in *Xironodrilus pulcherrimus* (Moore) and *Xironogiton occidentalis* Ellis.

Pierantoni (1912) says the internal segmentation would correspond

to the external as there are nine ganglia on the trunk portion of the nerve cord and the most posterior of these corresponds to three. He shows this last by tracing the nerves that have their origin in the posterior ganglion.

Schmidt (1905) thinks otherwise, believing the last ganglion corresponds to five. This then would make the total number of trunk segments thirteen. My own observations on this point have been in no way conclusive but they tend to support Pierantoni's view.

B. BODY WALL

The epidermis contains a great number of glands. Moore (1895b: 502) gives the best account of the epidermis and its glands in connection with his study of *Bdellodrilus illuminatus*:

The epidermis consists of ordinary epithelial cells, of non-nucleated protoplasm, and of gland cells, which are present in great number and variety. The epidermis proper presents little modification. The cellular elements are arranged with relation to the circular muscle fibers, which encircle the body walls at regular intervals and are so deeply imbedded in the epidermis that they are frequently almost in contact with the cuticle, only a thin layer of protoplasm separating them.

Concerning the epidermal glands, Moore (1895b:503) continues:

Glands are very richly developed in connection with the epidermis of *B. illuminatus*; and while all are constructed of similar elements, they differ much in size and arrangements of these elements. The elements are unicellular glands somewhat of the goblet cell type. In most cases they consist of an enlarged irregularly polyhedral body containing the nucleus, and tapering at one end into a slender, more or less elongated ductule. The only exceptions are those glands which are referred to as salivary and bursal glands.

Certain small mucous glands are very generally distributed over the skin; especially on the head, where they are regularly arranged in several transverse rows. They may be unicellular, or consist of three or four unicellular glands, the ductules of which are twisted or spiral.

On the sixth and seventh somites such glands become greatly increased in number and size; the body walls, particularly on the dorsal side, being little more than a thick glandular layer, which constitutes the clitellum. The unicellular glands are here aggregated in sub-globular or pyriform groups of from three to twenty or more, which extend inward to a length of from .03 mm. to .065 mm. Being arranged in a single stratum each cell forms part of the surface of the gland, close to which lies the deeply staining nucleus, in a mass of almost as deeply staining glandular protoplasm. The inner ends are glandular but clear and often unstained, and pass into ductules, which may be bound together into a fascicle, and either open in close proximity on the surface, or separate and open singly. In either case they wind a slightly spiral course, which is best seen in living animals, particularly when stained with methylene blue. The cell bodies have an average diameter of .011 mm., the ductules of .0018 mm., and a total length of about .05 mm.

The several cells in each group appear not to function simultaneously. Some have completely broken down into secretion while others are entirely protoplasmic.

Other masses of gland cells are developed in different parts of the epidermis. This is true in connections with the head, lips, and especially the posterior sucker. Concerning this last Moore (1895b:504) adds:

Glands similar to those described by Dörner, and more fully by Voigt, in *Branchiobdella*, are well developed in this species in relation to the posterior

sucker. The glandular masses, which largely fill the tenth and eleventh and part of the ninth somites, are pyriform, or aggregations of several pyriform groups. Large, granular, lightly staining cell bodies give rise to long slender ductules which, first united into fascicles, break up into smaller and smaller groups, and are finally distributed singly on all parts of the surface of the acetabulum. This arrangement is beautifully shown in living specimens. The ductules are filled with rounded granules, which may be forced from their mouths in living worms by pressure. The granules will emerge in strings, absorb water, swell, and run together in a very short time, forming a homogeneous mucus.

The body wall is then made up of epidermis, with its cuticular covering, and the muscle layers of circular and longitudinal muscle fibers. These muscle layers are arranged like those of most Oligochaeta with an outer circular and an inner longitudinal layer. According to Schmidt (1903), in *Branchiobdella* the cells of the circular layer regularly number twenty-five on each side of an ordinary segment; and each segment has its own system of longitudinal cells, forty-four in each half of the segment.

The cuticle is thin, transparent, colorless, nearly homogeneous and follows the epidermis, which secretes it, closely. It follows invaginations into the oral and sexual cavities. Cuticular markings are evident and appear to be different in different species. It is possible that these markings may furnish diagnostic characters. The writer hopes later to investigate this possibility.

The intersegmental septa, according to Moore, are formed of thin sheets of parallel dorso-ventral muscles arising from the ends of the longitudinal fibers. Septa practically disappear between the first four segments and are represented by thin slips that support the alimentary tract from the body walls. Septa are extremely well developed between the sexual somites.

The musculature of the posterior sucker is very well developed. Moore (1895b:509) says about *Bdellodrilus illuminatus*:

The musculature of the posterior sucker is complex, and well adapted to secure strength and mobility. The circular muscles undergo little change; but the longitudinal split up, by the branching of individual fibers, into a set which are the direct continuation of the body longitudinal fibers, a second set which pass dorso-ventrally across the body cavity, a third which radiate to the margins of the disc, and lastly a highly branched set which have become slightly displaced at their posterior ends, right or left from their original longitudinal direction, and consequently pass with a slight spiral turn from the body walls to the periphery of the sucker, where they cross and interlace with their fellows having an opposite displacement.

C. DIGESTIVE SYSTEM

The alimentary canal may be divided into several regions, the oral, pharyngeal, esophageal, intestinal, and anal. The mouth is situated between the lips into which the peristomium is divided. Aggregations of unicellular glands are developed from the margins and inner surfaces of the lips.

Posterior to these are slit-like dorsal and ventral infoldings of the epidermis and cuticle, bounded by a thickened epidermal pad. On the posterior walls of these invaginated pockets, the jaws are molded.

These jaws, one ventral and one dorsal, are solid chitinous plates. According to Ellis (1919:242) the primitive type is one with several sub-equal teeth. Modifications have progressed along one or both of two lines, namely, (a) reduction in number and (b) increase in size of some teeth correlated with reduction in size of others.

The jaws are provided with a powerful musculature. This is well described by Moore (1895b:511) for *Bdellodrilus illuminatus*:

The mechanism of the jaws is seen to be powerful and efficient. The muscular plates, with their radiating fibers, regulate the distance between the two jaws, approximating or separating them as the circular or radial fibers contract in turn. The circular muscles seem sufficiently powerful to bring the jaws together with crushing force. The protractor muscles carry the jaws forward (with a rotary or rocking movement on the muscular pads) against an object of attack, the lower jaw acting with its teeth as a hook, while the powerful retractor muscles of the upper jaw bring its toothed blade with a shearing motion between the ventral teeth. Thus is constituted an efficient pruning apparatus, the chief purpose of which is, I believe, the clipping off of branchial filaments of the crayfish host, from which the blood is then drawn. They are probably also used for mowing down the colonial infusorians which cluster along the borders of the branchial chamber, and remains of which are frequently seen with diatoms, etc. mixed with crayfish blood in the stomach of the worms examined.

The jaws mark the beginning of the pharyngeal region, which is characterized by great development of the musculature and which may function as a suction bulb. This region extends to the esophagus, which usually begins in the first body segment.

The esophagus is short and ill-defined. Its muscular coat is made of a sheet of circular and longitudinal muscles. This coat continues throughout the intestine, into which the esophagus rapidly merges. The intestine continues with various sacculations to the anus, situated in the dorsal half of segment X. In the second or third somite the peritoneum is modified to form chlorogogue cells which envelop the intestine except in the seventh somite. In the region of the dorsal blood vessel they arch over its walls. According to Moore (1895:513) they appear in surface view as "a mosaic of large polygonal cells, with straight closely fitted edges, possessing a large clear nucleus, and cytoplasm of a greenish brown color, due to the presence of numerous large granules and minute globules. In sections they appear more or less flattened, or prominently bulging, according to their position and the degree of contraction of the intestine." Being absent in the seventh segment they permit the maturing ova to come into close contact with the walls of the blood sinus, an important nutritive consideration.

The intestine in segments VIII and IX is a very narrow tube, the rectum. In the region of the anus the circular muscles increase to form a sphincter.

D. THE VASCULAR SYSTEM

According to Stephenson (1930:798) the vascular system of the Branchiobdellidae consists of a peri-enteric sinus, a dorsal and a ventral blood vessel, four pairs (three cephalic and one in front of the trunk) of vascular commissures in the anterior part of the body and one near the posterior end. Moore (1895b:514) found seven vascular arches present in *Bdellodrilus illuminatus*; four in the head and one each in segments I, VII, and IX. These connect the dorsal and ventral blood vessels.

In front of the third segment the dorsal vessel is large and pulsatile (the so-called heart) but posterior to this it loses its distinct identity and merges into the peri-enteric sinus. Moore (1895b:514) describes this sinus as follows:

The peri-enteric blood sinus, to which Voigt first especially called attention in Branchiobdella, is highly developed in the present species, in which it exists as a continuous space between the muscular and epithelial coats of the intestine, extending from the third to the eighth somites inclusive, and breaking up at each end into a system of passages and lacunae having a retiform arrangement. The sinus has an average depth of .005 mm., and is without true walls other than the intestinal coats between which it lies. It is crossed by numerous protoplasmic strands and columns which bind its walls together, and remind one of the stalactites and columns of a limestone cave. These become larger and more frequent towards the ends of the sinus, which they finally interrupt so much as to convert it into the terminal plexuses mentioned.

Throughout its entire length the ventral blood vessel lies in contact with the dorsal side of the nerve cord and passes through the ganglia of each segment in a deep groove. The ventral vessel terminates in the tenth segment in a pair of large trunks which arch around the intestine, and pass forward to empty into the dorsal region of the peri-enteric sinus, thus forming the beginning of the dorsal enlargement, which here receives the dorsal ends of the plexus of the blood passages.

Concerning the connecting lateral arches in *Bdellodrilus*, Moore (1895b:516) continues:

In the seventh somite it [the ventral blood vessel] gives off a pair of large ovarian vascular arches, which empty into the dorsal enlargement of the peri-enteric sinus. The supra-neural vessel terminates in the tenth somite in a pair of large trunks, which arch around the intestine, and pass forward to empty into the dorsal region of the peri-enteric sinus, thus forming the beginning of the dorsal enlargement, which here receives the dorsal ends of the plexus of blood passages. Of the seven pairs of lateral arches mentioned, a labial and three cephalic pairs, in the pharyngeal region, arise from the anterior prolongation of the heart; an oesophageal pair which owing to their great length are often looped into the succeeding somite, arise from the anterior end of the heart itself; a large pair of ovarian arches, which are more or less imbedded in the maturing ova, lie in the posterior part of the seventh somite; and the seventh pair, the largest of all, posteriorly connect the supra-neural vessel with the peri-enteric sinus. The walls of the supra-neural and lateral vessels are very delicate and non-contractile. At wide intervals, nuclei, which resemble those of the peritoneal cells, may be detected, but I have found no traces of cell boundaries.

E. RESPIRATORY SYSTEM

In the Branchiobdellidae, as in many aquatic Oligochaeta, there are no specialized organs of respiration. Respiratory exchange simply takes place in general through the body wall.

F. EXCRETORY SYSTEM

The excretory system of the group consists of two pairs of nephridia. Those of the anterior pair are placed asymmetrically and open in the dorsal part of segment III just behind septum II/III. They may open either through a single pore or through paired pores. As mentioned, they are not symmetrical, so the one may extend from segment III to I, and the other posteriorly from III to IV. The nephridia of the posterior pair are symmetrical and situated in segment VIII, opening to the outside just behind furrow VIII/IX.

The best accounts of the finer anatomy of the branchiobdellid nephridium are furnished by Moore (1897) and by Voinow (1896). These studies are well summarized by Stephenson (1930:224-226), who says:

Each nephridium begins in an open ciliated funnel, of which the lips are formed of two marginal cells; the single central cell bears a long ciliary flame, and unlike that of *Lumbricus* is tubular and surrounds the whole funnel below the marginal cells; this is followed by the stalk of the funnel, also composed of a single cell.

The next region constitutes the special peculiarity of the Branchiobdellid nephridium; it is called by Moore the plexus region. In the undisturbed condition of the organ it forms a compact lobulated mass; but when this is slightly teased apart it is seen to consist of a single tube, alternately swollen out and contracted; in each swelling there is a labyrinth of branching and anastomosing canals, while in each contracted part the lumen is single. At each contracted part is a nucleus, and here also on the inner surface of the wall is a ciliary flame; both nuclei and flames are absent from the parts occupied by the plexuses. The tube is to be considered as intracellular, the territory of each cell consisting of one of the narrowed sections of the tube and the adjacent parts of the swellings on each side. The plexus region is granular and yellowish and appears to be a seat of considerable excretory activity.

The looped portion of the organ succeeds the plexus region. It consists of two loops, a longer and a shorter, the longer with an irregular and twisted course, the shorter less tortuous. Each limb consists of a series of drainpipe cells, and the two limbs of a loop are apposed and mostly fused together. In the long loop are seen at intervals nuclei and accompanying ciliary flames—twelve of each; in the connecting tube between the two loops is a single nucleus and flame, and in the short loop ten nuclei but only one flame. On the inner surface of the tube in this region are seen peculiar minute rod-like markings, most numerous at the turning-point of the long tubule; these are occasioned by a lining coat of bacteria.

The wall of the long loop is only slightly granular, that of the short stains deeply and is very densely granular, the granules being disposed in radial lines. In the walls of the short tube, in the living organ, are seen granules exactly similar to others contained within the enlarged peritoneal cells which invest the loops, and similar granules occur also in its lumen. The cells, therefore, deposit solid particles in the lumen of the tube, in addition to passing in fluids containing matters in solution. Accumulations of disintegrated coelomic corpuscles are stated by Moore to be found in all parts of the nephridial lumen.

The duct passes along the plexus region, the zigzags of which are arranged on it as on a supporting axis, then surrounds the neck of the funnel in a small loop, undergoes a thickening of the wall in which are several small diverticula of the lumen, and enters the body wall. It consists of about ten cells, but no cilia.

The peritoneal covering is constituted by large cells with elongated processes extending outwards into the coelomic cavity. These cells apparently also take part in the excretory process.

G. THE NERVOUS SYSTEM

The branchiobdellids have a pair of supra-esophageal ganglia lying just posterior to the dorsal jaw pad. According to Moore the two ganglia are united across the median line by a cord of nerve cells and a fibrous commissure. Each bears posterior lobes which are in turn divided into large external and small internal parts and connected to the main ganglion by three strands of nervous tissue. The circum-esophageal connectives extend as thick strands of nerve fibers with a partial covering of nerve cells from the ganglia. They pass around the pharynx and each bears a bilobed stalked ganglion just before they join. They unite to form the ventral nerve cord, and just posterior to this anastomosis form two pairs of larger ganglia. This makes four pairs of double ganglia within the limits of the head (see four-segment head theory above).

Numerous nerve fibers arise from the circum-esophageal connectives and the supra-esophageal ganglion and pass forward to the peristomial region. These end in the circum-oral hairs and oral papillae.

The ventral nerve cord consists of two distinct halves throughout its length. It enlarges at the ganglia and narrows in the inter-gangliar intervals.

In the body segments there are eight pairs of bilobed ganglia and a posterior ganglionic mass called the anal ganglion. This ganglion is composed of several pairs of ganglia, three according to Moore and five according to Schmidt. The fifth and sixth ganglia are displaced to the right of the median line by the spermatheca and male atrium. Three pairs of nerves arise from the region of each pair of ganglia, one from each end and one from the transverse constriction. They supply the body walls, going between the two layers of muscles and splitting up as they proceed. The first and second nerves supply the major annulus; the third splits, one branch going also to the major annulus, the other branch supplying the minor annulus.

A thin muscular sheath encloses the nerve cord for its entire length and includes the ventral blood vessel.

H. THE REPRODUCTIVE SYSTEM

The male organs are situated in segments V and VI. In the genus *Branchiobdella* a pair of testes is present in segment V. In all other known genera an additional pair is present in segment VI. The sperms

are liberated directly into the body cavity, and in mature worms the testes cannot be detected. One or two pairs of vasa deferentia and funnels (depending on the number of testes) are present. The two vasa deferentia of each pair unite and all open within a single atrium. The atrium consists of a dilated ental portion and an ectal portion that is a narrow short bursa. The penis, which may or may not be eversible, is situated within the bursa. According to Michaelson, the atrium may be provided with glands near the place of entry of the vasa deferentia, but these are never compacted into a single prostate. In some genera an accessory sperm tube is present. This consists of a blind tube extending dorsally and anteriorly from the bursa.

The female reproductive system is situated in segment VII. A pair of ovaries is situated on the posterior face of septum VI/VII. In sexually mature worms large eggs are often present in segment VII. The oviducts are represented by two funnel-like pores in the ventro-lateral walls in the posterior part of segment VII. These pores are ciliated. A glandular clitellum forms about these genital segments. A spermatheca is present in segment V. It is unpaired and opens in the mid-ventral line about the middle of the segment. It is quite variable in form in different species. The blind end is usually free but may be attached by means of a peritoneal investment.

VI. RELATIONSHIPS OF THE BRANCHIOBDELLIDAE

FROM their general appearance, the presence of jaws, the absence of setae, and the posterior sucker, the Branchiobdellidae were originally considered leeches. Odier (1823) in the first taxonomic description of the group has a sub-title of "Nouveau Genre d'Annelides de la Famille des Hirudinées." Leidy (1851) and Verrill (1873) considered the American branchiobdellids to be leeches. They were omitted by Beddard (1895) in his monograph on the Oligochaeta, and Michaelsen (1900) failed to include them in his monograph in the Tierreich series. Later Michaelsen (1919b) insisted that they were Oligochaeta and closely related to the Lumbriculidae.

In 1903 F. Schmidt showed that the musculature in the Branchiobdellidae is definitely like that of the Oligochaeta and unlike that in most Hirudinea. Pierantoni (1912) in his monograph discussing their anatomy as Oligochaeta notes how closely they resemble *Mesoporodrilus*. Michaelsen (1919b) shows how the peculiar characters of the branchiobdellids are merely adaptations to parasitic life and could be derived from other Oligochaeta. The short body and posterior sucker are apparently adaptations to the habitat. The pharynx, he says, is a sucking apparatus, and the prostomium is absent. Both these characters are present in *Chaetogaster*, a

genus of Naididae the members of which are carnivorous and sometimes ectoparasitic. Michaelsen further compares the jaws to the pair of buccal stylets with chitinous tips in the buccal cavity of certain Enchytraeidae.

Since their genital organs are so much like those of the Lumbriculidae, it is generally agreed that they have a common origin with that family. Both these families have the combined male ducts opening to the outside on the segment that contains the hinder pair of testes. In many respects the Branchiobdellidae are only modified Lumbriculidae. Their relationships are shown in the accompanying diagram from Stephenson (1930:705).

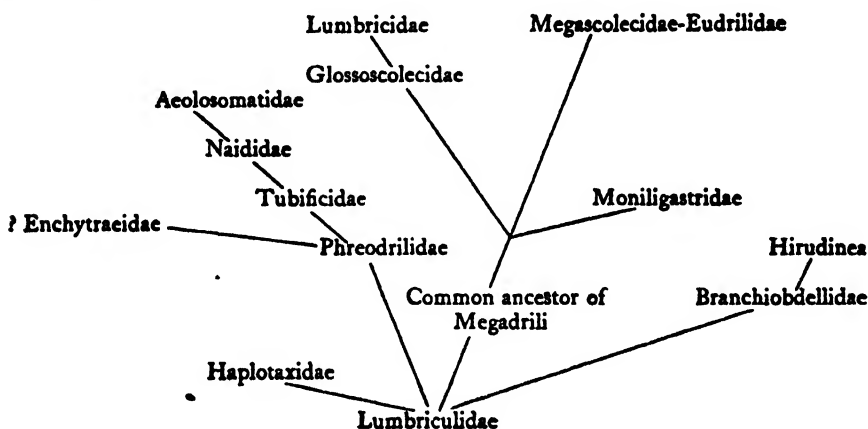


DIAGRAM OF RELATIONSHIPS (AFTER STEPHENSON, 1930)

Michaelsen (1919b:152) points out the similarity between leeches and oligochaetes and that the most significant difference is the position of the testes, posterior to the ovaries in Hirudinea and anterior in the Oligochaeta. So he proposes the following natural classification of annelids:

- KREIS ANNELIDES
- I. Klasse Archiannelides
 - II. Klasse Chaetopoda
 1. Ordnung Protochaeta
 2. Ordnung Polychaeta
 - III. Klasse Clitellata
 1. Ordnung Oligochaeta
 2. Ordnung Hirudinea
 - IV. Klasse Echiuroidea
 - V. Klasse Sipunculoidea

The two families, Branchiobdellidae and Acanthobdellidae, link the Oligochaeta and Hirudinea inseparably. Frank Smith (1920) reported this work in English, and at the time seemed to agree with the proposed classification.

VII. CHARACTERS OF TAXONOMIC SIGNIFICANCE

STEPHENSON (1930:796) calls the Branchiobdellidae a homogeneous group. However, even though they are very similar in structure, there are distinct generic and specific differences. Below are discussed the various morphological characters which the writer believes to be of diagnostic significance.

A. BODY SHAPE

While the shape of the body is somewhat variable it seems to correlate fairly well with other characters as a basis for generic description. For example, the flattened shapes of *Xironodrilus* and *Xironogiton*, as described above (page 13), are quite distinctive.

B. DORSAL APPENDAGES

The presence of distinct dorsal appendages, described above, has been used by Moore (1895a) as a generic character in establishing the genus *Pterodrilus* and followed by Ellis (1919) in describing additional species of this genus. Yamaguchi (1934:180) doubts the generic value and perhaps even the specific value of these dorsal appendages:

The dorsal appendages are known to be present in several species belonging to *Pterodrilus* and *Ceratodrilus*. According to Moore (1894) [1895a], *Pt. allicornus* and *Pt. disticus* are provided with dorsal transverse ridges and wing-like or cylindrical appendages located in the free margin of the ridges. *Ceratodrilus thysanosomus* also bears dorsal appendages extending from the dorsal transverse ridges (Hall, 1914). Digitiform dorsal appendages have been described in two Japanese species. *Stephanodrilus cirratus* and *St. uchidai*, which was at that time referred to *Ceratodrilus* (Yamaguchi, 1932a). The digitiform appendages of these species are mounted on dorsal transverse ridges which become lamelliform in *cirratus*, while in *uchidai* the ridges are rather inconspicuous so that the present writer overlooked them in his previous work (1932a). According to Moore (1894), the dorsal transverse ridges of *Pt. allicornus* are supported by dorsal segmental muscle fibers connecting the anterior with the posterior covering of hypodermis. Similar dorsal muscle fibers are also found in the dorsal transverse ridges of *cirratus* and *uchidai*. In the former species these fibers are quite conspicuous in highly developed ridges. The dorsal segmental fibers seen in these three species are found only on the dorsal side and are distinguishable from longitudinal muscles running the whole body length by their position and short length. The muscle fibers are probably identical to the "Langsmuskelzelle des Nebensystems" described by Schmidt (1903) in his study on the musculature of *Branchiobdella parasita*. *Stephanodrilus sapporensis* is destitute of dorsal appendages but is marked by a low conspicuous ridge supported by a few dorsal segmental muscles. In other species of *Stephanodrilus*, i.e., in *St. inukaii* n. sp., *St. megalodentatus* n. sp. etc., neither dorsal transverse ridges or dorsal appendages are present. The dorsal segmental muscles could not be detected in these species. From these facts it seems to the present writer that the dorsal ridges appear along with the development of the dorsal segmental muscles. In a previous paper (1932a) it is stated that in *Ceratodrilus uchidai* = *Stephanodrilus uchidai* the dorsal digitiform appendages are present in the six trunk somites III-VIII, each somite bearing twelve of them. As the result of examination on abundant specimens of the species collected from various localities it has been clear that there are several intergrades in regard both to number of somites bearing appendages and to the appendages on each somite. Some forms are also provided with appendages in the

six trunk somites III-VIII but they are variable in number according to the somites (maximum 12 and fewer in the more anterior ones). In others the appendages are more reduced in number and disappear in several anterior somites, finally disappearing altogether in all trunk somites. In these several forms the dorsal transverse ridges are always present accompanying the dorsal segmental muscle fibers. According to Ellis (1920) [1919] description and figures, *Pterodrilus durbani* seems to be also provided with dorsal transverse ridges, but to be destitute of distinct appendages except two "horns" found in the eighth trunk somite. Moreover, *Branchiobdella kobayashii* n. sp. has dorsal transverse ridges supported by dorsal segmental muscle fibers while *Br. orientalis* n. sp., and *Br. pentadonta* and others are destitute of the ridges. Judging from these facts, those provided with the dorsal transverse ridge, or dorsal segmental muscles, are not distinctly separated from those lacking them.

However, it seems to the writer that Yamaguchi's position is somewhat unjustified and that at least with the American forms the dorsal appendages are of generic significance. For example, in *Pterodrilus*, while there are specific differences, the appendages are similar enough to allow grouping into one genus. It seems that Yamaguchi has grouped forms diverse enough to be in several genera in the genus *Stephanodrilus*. In regard to *Stephanodrilus uchidai*, he is not even sure he is dealing with only one species. He merely says: "As the variation occurs in series all seem to belong to a single species."

C. PERISTOMIUM

The character of the peristomium appears to be of specific taxonomic value but not generic. Pierantoni (1912) believed the presence of a plurilobate peristomium to be of generic significance. Ellis (1919:256), when reviewing the genus *Cambarincola*, first expressed doubt of this view. He questioned it as follows:

One of these characters, "the plurilobate prostomium" is particularly noteworthy in this connection as it is used by Pierantoni to differentiate *Stephanodrilus* in his generic key. The two species *C. philadelphia* and *C. chirocephala* have lobate lips similar to the lips of *Stephanodrilus japonicus* Pierantoni as figured by Pierantoni. Neither *Stephanodrilus koreanus* Pierantoni nor *Stephanodrilus japonicus* Pierantoni, however, are figured with accessory sperm tubes, and the accessory sperm tube is present in species of *Cambarincola*. Pierantoni also figures *Branchiobdella digitata* Pierantoni, a species having but a single pair of testes (Pierantoni), with a plurilobate prostomium, showing that the lobate lip character occurs in that group of species.

Yamaguchi (1934:182) expresses the writer's view when he says:

The bilobate or pluri-lobed peristomium which was regarded as one of the generic characters by Pierantoni (1912) seems to be of no significance for generic value, because the two kinds of peristomia are found in one genus as will be stated below. In the genus *Branchiobdella* a pluri-lobed peristomium is found in *Br. digitata*, *Br. minuta* (Pierantoni 1912) and *Br. parasita* (Whitman 1882), while other species have a bilobed peristomium. On the other hand, *Cambarincola chirocephala*, *C. philadelphia* (Ellis 1920) [1919] and *C. okadai* (Yamaguchi 1933) are provided with a pluri-lobed peristomium, but other species belonging to the genus are provided with a bilobed peristomium. Though the present writer (1932a) distinguished the funnel-shaped peristomium from that not funnel-shaped, the distinction is not clear in several species.

D. JAWS

The number and arrangement of teeth on the jaws seem to be of specific importance, although there is considerable individual variation in some species. Variations in the dental formulae of several different species are given by Ellis (1919), from which the accompanying tables have been adapted.

TABLE I.—VARIATIONS IN THE DENTAL FORMULA OF *Xironodrillus formosus* ELLIS

Locality	Dental formulae					
	4-3	4-4	5-4	5-5	6-5	7-5
Irondale, Anderson, Ind.....	3	4	17	13	4	1
Noblesville, Ind.....	1	1	4
Charlevoix, Mich.....	1	..	2	..
Vincennes, Ind.....	2	1
<i>Number of specimens</i>	4	5	24	14	6	1

TABLE II.—VARIATIONS IN THE DENTAL FORMULA OF *Xironodrillus pulcherrimus* (MOORE)

Locality	Dental formulae				
	3-3	4-3	4-4	5-4	5-5
Blowing Rock, N. C.....	2
Cheat River, W. Va.....	2	6	..
Cheat Bridge, W. Va.....	3	..
Shavers Fork, W. Va.....	1	1
Cheat River, W. Va.....	1	8	..
Indian Creek, W. Va.....	1
Queens, W. Va.....	7	1
Trubies Run, W. Va.....	1	4	..
Baileyville, W. Va.....	1	..
<i>Number of specimens</i>	2	..	5	30	2

TABLE III.—VARIATIONS IN THE DENTAL FORMULA OF *Xironogiton oregonensis* ELLIS

Locality	Dental formulae					
	4-4	5-4	5-5	6-5	6-6	7-6
Eugene, Ore.....	1	8	3	2
Sequallitchew Lake, Wash.....	4	1	3
<i>Number of specimens</i>	1	8	3	6	1	3

From a total of 37 specimens of *Xironogiton instabilus* (Moore) examined from various localities in New York, Virginia, West Virginia, and North Carolina, Ellis found 16 with a 4-4 formula, 11 with a 5-4 formula, and 10 with a 5-5 formula.

We could go on citing other species, the great variation in formulae of *Cambarincola philadelphica* (Leidy), etc., but this is sufficient to show that in nearly all species sufficiently studied there is a great diversity of dental formulae.

However, in spite of this variation, individual formulae are sufficiently similar to be of specific importance. In fact Yamaguchi (1934:184) suggests that in some cases the dentition may be of generic importance when he uses it as a character to separate *Stephanodrilus* and *Cambarincola* as follows:

	<i>Stephanodrilus</i>	<i>Cambarincola</i>
Dorsal dental plate. . .	Provided with seven or more teeth, median one larger than lateral ones.	Provided with five teeth, a large median and four small lateral ones.
Ventral dental plate. . .	Similar in dentition to the dorsal plate.	Provided with four teeth, having no median unpaired teeth (except in <i>C. okadai</i> bearing same dentition as dorsal plate).

The writer considers the dentition and general shape of the jaws to be of specific but not generic importance.

E. POSITION OF CAUDAL SUCKER

Whether the sucker is ventral, as in *Xironodrilus*, *Xironogiton*, etc., or terminal, as in *Cambarincola* and others, seems to be of some generic significance when correlated with the general shape of the body.

F. SHAPE OF GUT

While the gut varies considerably in shape, depending on the amount of food present and the amount of contraction of the specimen, its general shape may in some cases be used as an additional specific diagnostic character. However, it is not an important taxonomic character.

G. PHARYNGEAL DIVERTICULA

Ellis (1919:243) says:

From the sections studied the number and position of the major pharyngeal diverticula and the presence or absence of buttress-like supports of connective tissue attached to the intersegmental partitions were considered of taxonomic value. The major pharyngeal diverticula may be seen to best advantage in sagittal sections but may be located in good whole mounts of compressed worms. These pharyngeal diverticula are not to be confused with the slight invaginations of the pharyngeal wall nor with the fold in the pharyngeal wall near the posterior end of the pharynx (found in many preserved specimens), due to the pushing forward of the esophageal portion of the alimentary canal so that the anterior end of the esophagus partly telescopes the posterior end of the pharynx.

But Yamaguchi (1934:183) throws doubt on the importance of pharyngeal diverticula:

But it was difficult for the present writer to distinguish the "major pharyngeal diverticula" from the "slight invaginations." It seems to be quite doubtful, therefore, whether one should consider the number and position of the "major pharyngeal diverticula" as an important taxonomic character.

The writer agrees with Yamaguchi that their taxonomic value is doubtful.

H. OPENING OF THE ANTERIOR NEPHRIDIA

The paired or unpaired condition of the pores by which the anterior nephridia open to the outside seems to be of generic importance. For example, *Cambarincola* has a single pore while *Xironodrilus*, *Xironogiton*, and *Branchiobdella* have paired pores.

In the genus *Stephanodrilus*, Yamaguchi (1934) has described *S. koreanus* Pierantoni as having a single pore while all the remaining species of the genus have paired pores. But here again, in this diverse genus, several genera may well be included.

I. NUMBER OF TESTES

The genus *Branchiobdella* is separated from all other genera by the presence of a single pair of testes located in segment V. All other known genera have two pairs located in segments V and VI. This has been the basis of separating the two subfamilies, *Branchiobdellinae* and *Cambarincolinae*.

J. ACCESSORY SPERM TUBE

The accessory sperm tube, described by Ellis (1912) as a generic character of *Cambarincola*, consists of a blind tube arising from the spermathecal vesicle and extending anteriorly. This is, according to Yamaguchi, homologous to the blind tube present in other species of other genera. It is very distinct and can clearly be seen in cleared whole mounts. It seems to be of generic importance, occurring in the genera *Cambarincola* and *Xironogiton*.

K. PENIS

Certain genera, as *Cambarincola*, appear to have non-eversible penes, while others, as *Cirrodorilus*, are eversible. The character of the penis provides characters which are constant within certain groups, and therefore seems to be of generic significance.

L. SHAPE OF THE SPERMATHECA

The various shapes of the spermatheca seem to be of specific significance but have no generic importance with possibly one exception, namely, the bifid spermatheca of *Bdellodrilus*. However, only one species of this genus is known, and further study may reveal that this character is of specific value only.

VIII. CLASSIFICATION OF THE AMERICAN
BRANCHIOBDELLIDAE

IN THE FOLLOWING classification, the characterizations of the Class and Order are translations from Michaelsen (1919:153).

PHYLUM ANNELIDA.—Triploblastic coelomate worms characteristically having a metanephridial excretory system, a ventral nervous system, and a dorsal blood vessel. Segmentation is typical but not universal.

CLASS CLITELLATA.—Annelids with well-developed outer and inner metamerism, without parapodia, and without feelers, tactile cirri and ordinary cirri, mostly without gills; hermaphroditic. Gonads in a few definite segments. Clitellum present. Development is direct; in the main, fresh-water and land animals.

ORDER OLIGOCHAETA.—Clitellum present, mostly with setae in the skin. Segments mostly single or slightly and unequally divided. Coelom well developed, large. Testes anterior to the ovaries, generally one or two pairs.

SUPERFAMILY BRANCHIOBDELLOIDEA Hall, 1914

Body divided into two regions, a head and a trunk, the latter terminated by a sucker; without setae; mouth provided with two chitinous jaws; two pairs of nephridia; testes in pairs in fifth or in fifth and sixth segment; ovaries in the seventh segment; unpaired spermatheca in the fifth.

FAMILY BRANCHIOBDELLIDAE

With the characteristics of the superfamily.

In the present study the writer has become impressed with the fact that the family Branchiobdellidae contains two distinct groups of genera. The sharpness of this distinction warrants the recognition of two separate subfamilies. In proposing Branchiobdellinae and Cambarincolinae as new subfamilies, the following diagnosis is presented:

BRANCHIOBDELLINAE.—Branchiobdellidae with only one pair of testes, located in the fifth segment.

CAMBARINCOLINAE.—Branchiobdellidae with two pairs of testes, located in the fifth and sixth segments.

SUBFAMILY BRANCHIOBDELLINAE new subfamily

Branchiobdellid worms having one pair of testes and male funnels located in the fifth segment.

Type and only genus: *Branchiobdella* Odier, 1823.

GENUS BRANCHIOBDELLA Odier, 1823

Branchiobdella, Odier 1823. Mem. Soc. d'Hist. Nat. de Paris 1:75.

Branchiobdella, Pierantoni 1912. Ann. Mus. Zool. Univ. Napoli, N.S. 3(24):9.

Branchiobdella, Stephenson 1930:800.

Branchiobdella, Yamaguchi 1934. Jour. Fac. Sci. Hokkaido Imp. Univ. 3:185.

With the characteristics of the subfamily; spermatheca simple, not bifid; penis eversible; no accessory sperm tube; anterior nephridia opening to the outside by separate pores in segment III; body cylindrical, not flattened; without body appendages.

Type species: *Branchiobdella astaci* Odier, 1823, from western Europe.

KEY TO AMERICAN SPECIES OF THE GENUS BRANCHIOBDELLA

1. Dorsal and ventral jaws dissimilar with a 5-4 dental formula; peristomium entire.....*Branchiobdella americana* Pierantoni, 1912
2. Dorsal and ventral jaws similar with a 4-4 dental formula; peristomium bilobed.....*Branchiobdella tetradonta* Pierantoni, 1906

Branchiobdella tetradonta Pierantoni, 1906

Branchiobdella tetradonta, Pierantoni 1906b. Ann. Mus. Zool. Univ. Napoli, N.S. 2(11).

Branchiobdella tetradonta, Ellis 1912. Proc. U.S.N.M. 42:485.

Branchiobdella tetradonta, Pierantoni 1912. Ann. Mus. Zool. Univ. Napoli, N.S. 3(24).

Description (based on Pierantoni 1912):

Peristomium divided into two lips, a dorsal and a ventral; head distinctly separated from body. Body rather uniform throughout, not enlarged in median portion. Posterior sucker cup-like, not very prominent.

Length about 2.0 mm.

Jaws similar, bearing four equal teeth placed in a row, the two median ones sometimes a little shorter than the outer ones.

Spermatheca shaped like an hour glass, with a short passage tube "condotto di uscita." Atrium enlarged and sack-shaped.

Type: From Klamath River, Calif., on *Astacus klamathensis*.

Previous locality record: Pierantoni, 1906b, N.S. 2 (No. 11)—Klamath River, Calif., on *Astacus klamathensis*.

Remarks: The present writer has not examined this form.

Branchiobdella americana Pierantoni, 1912

Branchiobdella americana, Pierantoni 1912. Ann. Mus. Zool. Univ. Napoli, N.S. 3(24):1-20.

Branchiobdella americana, Hall 1914. Proc. U.S.N.M. 48:190-192.

Description (based on Pierantoni 1912):

Peristomium entire, a little enlarged to form a sucker; head very distinct from body, circumbuccal ring of papillae present; body not

"swollen" towards the middle; body semi-cylindrical; posterior sucker slightly prominent; clitellum slightly visible.

Length about 5.0 mm.

Jaws unequal, the dorsal provided with a large median tooth and with two pairs of smaller median teeth; the ventral with two large teeth and two smaller ones.

The spermatheca in this species is in the form of an hour glass with short neck; without terminal process. The male atrium is slightly enlarged.

Type: Material from Texas on *Cambarus viridis* (according to Pierantoni), *C. latimanus*, and *C. hayi*, and from Raleigh, N. C., on *C. rusticus*, *C. immunis*, and *C. sp.*

Previous locality records:

Pierantoni 1912, N.S. 3(24)—

1. Texas, on *Cambarus viridis*, *C. latimanus*, and *C. hayi*.

2. Raleigh, N. C., on *C. rusticus*, *C. immunis*, and *C. sp.*

Allen 1933:119—

1. Durham, N. C.

New locality records:

1. Cleveland, N. Y., on *Cambarus bartoni robustus*.

Remarks: The material examined by the writer from Cleveland, N. Y., agreed very well with the above description. However Pierantoni failed to mention the large everted penis, which was quite evident in the writer's specimens.

SUBFAMILY CAMBARINCOLINAE new subfamily

Branchiobdellid worms having two pairs of testes and male funnels located in the fifth and sixth segment.

Type genus: *Cambarincola* Ellis, 1912.

KEY TO THE GENERA OF SUBFAMILY CAMBARINCOLINAE

1. (a) Body with appendages.....2
- (b) Body without appendages.....3
2. (a) Appendages in the form of blunt cylindrical projections along the median dorsal line of body.....*Pterodrilus* Moore, 1895
- (b) Appendages in the form of pointed bands encircling the dorsal surface of the body.....*Cirrodrilus* Pierantoni, 1905
3. (a) Accessory sperm tube present.....4
- (b) Accessory sperm tube absent.....5
4. (a) Body cylindrical, not flattened, posterior end not conspicuously enlarged, anterior nephridia opening to the outside through a single pore.....*Cambarincola* Ellis, 1912
- (b) Body flattened, posterior end enlarged, so that body is racket- or spatula-shaped, anterior nephridia opening to the outside through separate pores.....*Xironogiton* Ellis, 1919
5. (a) Pair of large clear glands in each of the nine postcephalic segments; spermatheca bifid.....*Bdellodrilus* Moore, 1895
- (b) Without a pair of large clear glands in each of the nine post-cephalic segments; spermatheca not bifid.....6

- 6. (a) Major annulations of body segments secondarily divided especially noticeable in the median segments.....Triannulata new genus
- (b) Major annulations of body segments not secondarily divided.....7
- 7. (a) Body flattened; sucker ventral.....Xironodrilus Ellis, 1919
- (b) Body not flattened; sucker terminal.....Stephanodrilus Pierantoni, 1906

GENUS CAMBARINCOLA Ellis, 1912

Astacobdella, Leidy 1851. Proc. Acad. Nat. Sci. Phila. 206.
 Branchiobdella (in part), Moore 1894. Proc. Acad. Nat. Sci. Phila. 427-428.
 Bdelodrilus (in part), Pierantoni 1912. Ann. Mus. Zool. Univ. Napoli, N.S. 3(24).
 Cambarincola, Ellis 1912. Proc. U.S.N.M. 42:481-485.
 Cambarincola, Hall 1914. Proc. U.S.N.M. 48:190-192.
 Cambarincola, Ellis 1919. Proc. U.S.N.M. 55:255-264.
 Cambarincola, Stephenson 1930:801-802.
 Cambarincola, Yamaguchi 1932c. Proc. Imp. Acad. 8(9):454-456.
 Cambarincola, Yamaguchi 1933. Proc. Imp. Acad. 9(4):191-193.
 Cambarincola, Yamaguchi 1934. Jour. Fac. Sci. Hokkaido 3(3):189-191.

With the characteristics of the subfamily; spermatheca simple, not bifid; accessory sperm tube present; bursa but not penis eversible; anterior nephridia opening to the outside through a common pore situated on a median dorsal papilla; body cylindrical not flattened; without body appendages.

Type species: *Cambarincola macrodonta* Ellis, 1912.

KEY TO THE SUBGENERA OF CAMBARINCOLA

- 1. Upper lip composed of four subequal lobes.....Coronata new subgenus
- 2. Upper lip entire excepting a small median emargination.....
 Cambarincola new subgenus

SUBGENUS CAMBARINCOLA new subgenus

With the characteristics of the genus *Cambarincola*; upper and lower lip entire excepting a small median emargination in all but *C. inversa* which has two small lobes in the base of the emargination.

Type species: *Cambarincola macrodonta* Ellis, 1912.

KEY TO THE AMERICAN SPECIES OF THE SUBGENUS CAMBARINCOLA

- 1. (a) Major annulation of segment VIII visibly and distinctly elevated over minor annulations.....*Cambarincola elevata* new species
- (b) Major annulations of segment VIII not distinctly elevated over minor annulation.....2
- 2. (a) Upper jaw with three prominent teeth; if, as in a few specimens, five teeth are present the two lateral ones are very small.....
 *Cambarincola inversa* Ellis, 1919
- (b) Upper jaw not as above but with five noticeable teeth.....3
- 3. (a) Middle tooth of upper jaw long and prominent when compared with the small lateral teeth.....*Cambarincola macrodonta* Ellis, 1912
- (b) Middle tooth of upper jaw longer than the other four teeth but small enough that all five teeth may be considered subequal.....
 *Cambarincola vitrea* Ellis, 1919

Cambarincola (*Cambarincola*) *macrodonta* Ellis, 1912

Cambarincola macrodonta, Ellis 1912. Proc. U.S.N.M. 42:481-486.

Cambarincola macrodonta, Hall 1914. Proc. U.S.N.M. 48:190.

Cambarincola macrodonta, Ellis 1919. Proc. U.S.N.M. 55:257.

Description from Ellis 1912:481-486:

"Body rather slender when extended, slightly arched ventrally, circular in cross section in all regions, greatest diameter in the fifth or sixth segment, shortest diameter in the first segment, sloping gradually from the fifth segment to the first and rather abruptly from the sixth segment to the acetabulum; greatest diameter of the head always less than the greatest diameter of the body; greatest diameter of the body 5 to 8 in the body length; head distinct, elongate in extended specimens; length of the head greater than the greatest diameter of the body in extended specimens (greatest diameter of the body 1.1 to 1.3 in the length of the head), equal to or less than the greatest diameter of the body in contracted individuals (length of the head 1 to 1.3 in the greatest diameter of the body); greatest diameter of the head 1.2 to 1.4 in the greatest diameter of the body.

"Head composed of four annulations; the first or anterior cephalic annulation very prominent, of less diameter than the second annulation, tapering forward, from 2.3 to 3.3 in the total length of the head, depending upon the degree of contraction, composed largely of two fleshy lips—a dorsal and a ventral—of which the dorsal is very slightly the longer; the other three annulations very indistinctly marked, so that the remainder of the head appears to be but a single piece; first seven or eight body segments showing a rather distinct biannulation, the anterior portion of each segment being of the greater diameter; acetabulum terminal, of moderate size, from 1 to 1.25 in the greatest diameter of the head; genital papillae on segments 5 and 6, quite conspicuous in large specimens.

"Mouth terminal, or very slightly ventral, its opening rather diamond shaped, with the greatest dimension at right angles to the dorso-ventral line, guarded by two large lips, each of which bears several tiny papillae on its inner surface and a few minute hairs on its outer edge near the median line; each lip entire with the exception of a single slight emargination in the median line, which may be entirely wanting; dental plates very dark-brown to black, situated at or just in front of the junction of the first and second cephalic annulations; dorsal plate roughly triangular in outline when seen from the front, middle portion of the base excavated so that the two corners extend beyond the rest of the plate as two horns, anterior face with two rather prominent teeth on each side near the edge of the plate, the tooth nearer the apex on each side being pointed and larger than the basal tooth, apex produced into a single large cylindrical tooth with a conical point; ventral plate with an excavated base like that of the dorsal plate, the anterior face bearing a single small

knob-shaped tooth on each side near the base, apex produced into two large cylindrical teeth, each with a conical point.

"Pharynx narrowing just behind the dental plates, with a distinct dorsal diverticulum near the junction of the second and third cephalic annulations and a ventral diverticulum slightly caudad, the mouths of the two diverticula producing an irregular enlargement of the pharynx in the third annulation; esophagus narrow, occupying the first body segment, near the middle of which it drops to the floor of the body cavity; crop or post-esophageal portion of the alimentary canal extending through segments 2 and 3, rising gradually to the center of the body, increasing steadily in diameter, caudad, and showing little or no constriction at the junction of segments 2 and 3 unless distended with food; stomach large, almost filling segment 4, marked off by definite constrictions; intestine proceeding as a straight tube of slightly less diameter than that of the stomach through the center of segments 5 and 6; in segment 7 becoming somewhat narrowed, swinging dorsally and to the left side of the body in the anterior portion of the segment, and returning much narrower to the right of the median line in the posterior portion of the segment, leaving segment 7 near the dorsal wall of the body cavity; continuing in the anterior portion of segment 8 much narrower, crossing again to the left side and descending to the center of the segment, enlarging in the posterior portion of the segment, but leaving segment 8 near the center as a small tube; the rectum beginning in segment 9, passing diagonally through this segment to its dorsal wall, opening dorsally in the median line in the anterior portion of segment 10.

"Living animals colorless and quite transparent excepting the alimentary canal (which was a pale green in the specimens observed), and the gonads; body quite contractile."

Type: U.S.N.M. No. 53794 from Boulder, Colo., on *Cambarus diogenes* Girard. Length 4.65 mm.

Previous locality records:

Ellis 1912:481—

1. Boulder, Colo., on *Cambarus diogenes*.

Ellis 1919:251—

1. Fort Clark, Tex., on *C. clarkii*.
2. New Orleans, La., on *C. diogenes ludovicianus*.
3. Sims Bayou, Houston, Tex., on *C. blandingii acutus*.
4. Lake Lapoudre, Morgan City, La., on *C. clarkii*.
5. Frierson, La., on *C. blandingii acutus*.
6. Las Vegas, N. M., on *C. gallinas*.
7. Muldon, Miss., on *C. hagenianus*.
8. Black Wolf Creek, near Beecher's Island, Colo., on *C. diogenes*.
9. Arikaree River near Beecher's Island, Colo., on *C. diogenes*.
10. Boulder, Colo., on *C. diogenes*.

New locality records:

1. Leaf River, Ill., on *C. virilis*.
2. Macoupin Co., Ill., on *C. virilis*.

3. Champaign Co., Ill., on *C. virilis*, *C. immunis*, and *C. propinquus*.
4. Oakwood, Ill., on *C. propinquus*.
5. Botetourt Co., Va., on *C. bartonii*.
6. Mena, Ark., on *C. menae*.
7. Dent Co., Mo., on *C. medius*.
8. Omaha, Neb., on *C. immunis*.

Remarks: The above quotation describes very accurately this species which has little variation despite its large geographical range.

Cambarincola (Cambarincola) vitrea Ellis, 1919

Cambarincola vitrea, Ellis 1918. Trans. Amer. Micr. Soc. 37:49-51.

Cambarincola vitrea, Ellis 1919. Proc. U.S.N.M. 55:257-258.

Description from Ellis 1919:257-258:

"Body and head subterrate, little if at all depressed; diameter of the head approximately equal to that of segment II, usually slightly greater than that of segment I; body segments II to VIII subequal, segments V, VI, and VII when distended with sex cells slightly wider than segments III and IV; segments posterior to VIII narrowing rather rapidly to the caudal sucker, the diameter of which is less than of the head; all body segments easily visible in side view; major annulations distinct, but very slightly elevated above the minor annulations; head divided into three subequal parts, the anterior being the most distinct of the three; lips two, subequal, each with a small, median emargination; major pharyngeal diverticula two, the dorsal slightly anterior to the ventral; a few short bristles present on each lip; dental formula 5-4; . . . alimentary canal straight, following the mesial line of the body, maximum enlargement in segment IV; anterior nephridia opening to the outside through a common pulsatile pore on the dorsal surface of the major annulation of segment III; spermatheca simple and tubular; testes present in segment V and VI, vasa deferentia from segments V and VI meeting the atrium in segment VI; accessory sperm tube present; largest specimen examined, 4.7 mm.

"This species superficially resembles *Xironodrilus formosus* Ellis, both in body form and type of jaws. In addition to the several generic characters by which these two species may be separated, it may be noted that the jaws, although having the same number of teeth and the same general form, are quite different."

Type: U.S.N.M. 17668 from Douglas Lake, Mich., on *Cambarus virilis* Hagen. Length: 310 mm.

Previous locality records:

Ellis 1918:49-51—

1. Douglas Lake, Mich., on *Cambarus virilis*.
2. James Island, Potagannissing Bay, Mich., on *C. virilis*.
3. Three miles up Potagannissing River, Drummond Island, Mich., on *C. virilis*.
4. Sault Sainte Marie, St. Marys River, Mich., on *C. propinquus*.
5. Echo Lake, Grand Island, Lake Superior, Mich., on *C. propinquus*.

Ellis 1919:257-258—

1. Rhinelander, Wis., on *C. virilis*.
2. St. Vrain, Colo., on *C. immunis*.
3. Rolla, Mo., on *C. virilis*.
4. Maple River, Douglas Lake, Mich., on *C. propinquus*.
5. Lake Huron, Cheboygan, Mich., on *C. propinquus* and *C. virilis*.
6. Grapevine Point, Douglas Lake, Mich., on *C. propinquus*.
7. Wellington, Ill., on *C. virilis*.
8. Urbana, Ill., on *C. virilis*.
9. Arikaree River, near Beecher's Island, Colo., on *C. virilis*.
10. St. Marys River, Fort Wayne, Ind. (host not given).
11. Mouth of Carp River, St. Martins Bay, near Straits of Mackinac, on *C. virilis*.

New locality records:

1. Leaf River, Ill., on *C. virilis*.
2. Lake Geneva, Wis., on *C. virilis*.
3. Macoupin County, Ill., on *C. blandingii acutus*, *C. virilis*, *C. immunis*, and *C. propinquus*.
4. Oakwood, Ill., on *C. propinquus*.
5. Punta Gorda, Fla., on *C. sp.*
6. Stillwater, Okla., on *C. sp.*
7. Tuscaloosa, Ala., on *C. sp.*
8. Cleveland, N. Y., on *C. bartonii*.
9. Alpha, Ky., on *C. placidus*.
10. Odessa, Mich., on *C. propinquus*.
11. Indianapolis, Ind., on *C. rusticus*.
12. Lisbon, N. D., on *C. virilis*.
13. Dallas, Tex., on *C. simulans*.
14. Hayward, Wis., on *C. virilis*.
15. Marathon, Wis., on *C. virilis*.
16. Pittsville, Wis., on *C. virilis*.
17. Glen Flora, Wis., on *C. virilis*.
18. Swastika, Ontario, on *C. virilis*.
19. Holcombe, Wis., on *C. virilis*.
20. Noxubee County, Miss., on *C. mississippiensis*.
21. Galloway, Mo., on *C. longidigitus*.
22. Emette Co., Mich., on *C. propinquus*.
23. St. Marys River, Ontario.

Remarks: This form could be confused with *Cambarincola macrodonta*, but it is easily distinguished by the difference in tooth structure as outlined above.

Cambarincola (Cambarincola) elevata new species

(Pl. I, Fig. 3; Pl. II, Fig. 5)

Description:

Length of mature worms varying between 2.0 and 3.0 mm. The head diameter approximately equal to segment II, slightly greater than segment I. Segments increasing in diameter to segment VI or VII which is about 0.4 mm. in a worm 2.5 mm. long, then decreasing rapidly to the caudal sucker, whose diameter is slightly less than the head; sucker terminal; body little if at all depressed. Major annulations distinct; all

except segment VIII but very slightly elevated over minor annulations; major annulation of segment VIII distinctly and visibly elevated over the minor annulation so as to almost obscure it.

Head divided into three subequal parts; peristomium divided into two lips each with a slight median emargination. Jaws small, about 15-20 microns in a 2.5 mm. worm with a tooth formula of 5-4. The alimentary canal is straight following the mesial line of the body with the maximum enlargement in segment IV; anus present in the dorsal half of segment X.

Two pairs of testes present, one pair in segment V and one pair in VI; vasa deferentia joining the atrium in VI; distinct accessory sperm tube present in VI. Bursa but not penis eversible. Ovaries in segment VII; spermatheca in V consists of three parts, a short muscular portion near the spermathecal pore, a short middle tubular portion, and large dorsal globose part, resembling the spermatheca of *Xironodrillus formosus*; anterior nephridia opening to the outside through a common pore in the dorsal half of segment III.

Holotype: From Leaf River, Ill. on *Cambarus virilis*.

Paratypes: From Macoupin Creek near Carlinville, Ill., on *Cambarus virilis*; Buck Creek near Penfield, Ill., on *C. virilis*; Leaf River near Byron, Ill., on *C. virilis*; Seven Mile Creek, Rock River Drainage, Ill., on *C. virilis* and *C. propinquus*; and Lake Geneva, Wis., on *C. virilis*.

Additional material: Farmington, Mo., on *C. punctimanus*; Iowa River, Iowa, above Junction of Upper Iowa River; Oxford, Ontario.

Remarks: This species is closely related to *C. vitrea*, but differs in the elevation of the major annulation of segment VIII and in the shape of the spermatheca which is simple and tubular in *C. vitrea*. The holotype will be deposited in the United States National Museum, and paratypes in the collection of Dr. H. J. Van Cleave, of the University of Illinois, and in the collection of the writer.

Cambarincola (Cambarincola) inversa Ellis, 1919

Cambarincola inversa, Ellis 1919. Proc. U.S.N.M. 55:259-260.

Description from Ellis 1919:259-260:

"Body rather elongate and more or less terete; width of the head approximately equal to that of segment I; body segments increasing in width regularly and gradually from segment I to segment VI, which is the widest segment of the body; segments VII and VIII slightly narrower than segment VI; body posterior to segment VIII narrowing rapidly to the caudal sucker; all eleven body segments visible in side view and nine or more visible in dorsal view; caudal sucker termino-ventral, its diameter less than that of the head; each segment slightly constricted anteriorly and posteriorly, so that the segmental junctions are distinct; head subcylindrical, its anterior third defined by a groove or constrict-

tion; length of the head in a moderately expanded specimen slightly less than the length of the first two body segments; lips, two, the upper slightly longer than the lower; the lower lip with a distinct median emargination; upper lip like the lower, but with two small lobes in the base of the emargination; oral bristles present; dental formula 3-4, varying 3-3 to 5-4; upper jaw with three large teeth, of which the middle one is the longest, all three directed forward—that is, away from the base of the jaw; dental ridge of the upper jaw usually with a small tubercle in the position of the teeth of the “e” order—that is, if the jaw were five-toothed (teeth were found on these tubercles in two specimens, the tooth point in each case being very small); lower jaw with two large teeth and two small lateral teeth; upper jaw 20 micra wide, lower jaw 17 micra wide in an expanded worm measuring 3.6 mm.; major pharyngeal diverticula two, one dorsal and one ventral; anterior nephridia alternating in segments II and III, opening to the outside in segment III through a common pore in the dorsal surface of the major annulation of segment III; spermatheca simple, long, and tubular, not bifid; testes present in segments V and VI, vasa deferentia from segments V and VI meeting in the strium in segment VI; alimentary canal straight, increasing in diameter in segment I, much expanded in segments II, III, and IV, in which segments it forms an almost continuous pouch; intestine narrowing in the posterior half of segment IV; alimentary canal following the mesial line of the body through segments V to IX, swinging dorsad through segment IX to anal opening on the dorsal surface of segment X.”

Type: U.S.N.M. No. 17680 from Eugene, Ore., on *Astacus klamathensis*.

Previous locality records:

Ellis 1919:259—

1. Eugene, Ore., on *Astacus klamathensis*.

New locality records:

1. Twenty-two miles from Vintago, Wash., on *A. sp.*
2. Klamath, Ore., from *A. trowbridgii*.
3. Deer Creek, Ore., on *A. klamathensis*.
4. Yakima, Wash., on *A. klamathensis*.
5. Bovill, Idaho, on *A. gambelii*.
6. Minam, Ore., on *A. klamathensis*.
7. Odessa, Wash., on *A. klamathensis*.
8. St. Helens, Ore., on *A. trowbridgii*.
9. Lew Co., Wash., on *A. trowbridgii*.
10. Cestsajo Creek, Ore., on *A. trowbridgii*.
11. Redmond, Wash., on *A. trowbridgii*.
12. Vernonia, Ore., on *A. trowbridgii*.
13. Silver Creek, Harney County, Ore., on *A. gambelii*.
14. Young River, Ore., on *A. klamathensis*.

Remarks: Although a great many specimens were studied, little variation was encountered.

SUBGENUS CORONATA new subgenus

With the characteristics of the genus *Cambarincola*; upper lip composed of four subequal lobes, which may be extended as digitiform tentacles; lower lip composed of two subequal lobes which may be extended also; middle tooth of upper jaw long and prominent, almost obscuring lateral ones.

Type species: *Cambarincola philadelphica* (Leidy, 1851)

KEY TO THE AMERICAN SPECIES OF THE SUBGENUS CORONATA

1. Major annulations of body segments distinctly and visibly elevated over minor annulations.....*Cambarincola chirocephala* Ellis, 1919
2. Major annulations of body segments not elevated over minor annulations.....*Cambarincola philadelphica* (Leidy, 1851)

Cambarincola (Coronata) chirocephala Ellis, 1919

Cambarincola chirocephala, Ellis 1919. Proc. U.S.N.M. 55:263-264.

Description from Ellis 1919:263-264:

"General body form that of *Cambarincola philadelphica* (Leidy); body segments evident, major annulations of segments especially in contracted specimens, distinctly and visibly elevated above the minor annulations; body segments increasing regularly and gradually in diameter from segment I to segment VI or VII, and decreasing slightly from segment VIII to the caudal suckers; body terete; head large, equalling the first two body segments in length and exceeding the first segment in width; lips two, upper composed of four subequal lobes which may be extended into four distinct digitiform tentacles, or may be so flattened as to give the lip an almost entire outline; lower lips of two larger, subequal lobes which are usually somewhat extended; a very small intermediate lobe at the junction of the upper and lower lip on each side of the mouth; major pharyngeal diverticula two, a dorsal and a ventral, the dorsal diverticulum being slightly cephalad of the ventral; dental formula 5-4; upper jaw very large, its width two or three times that of the lower jaw, teeth of the "a" and "b" orders on each side very small, less than one-sixth of the height of tooth "a." The jaw appearing to have but one tooth when examined under low power magnification; . . . anterior nephridia opening to the outside through a common pore in segment III; spermatheca simple, bulbous; testes in segments V and VI, vasa deferentia from segments V and VI meeting in segment VI."

Type: U.S.N.M. No. 17713, from Rolla, Mo., on *Cambarus virilis*.

Previous locality records:

Ellis 1919:263—

1. Rolla, Mo., on *Cambarus virilis*.

New locality records:

1. Leaf River, Ill., on *C. virilis*.
2. Campaign County, Ill., on *C. virilis*, *C. blandingii acutus*, and *C. propinquus*.
3. Oakwood, Ill., on *C. propinquus*.
4. Cleveland, N. Y., on *C. bartonii*.
5. Oxford, Ontario, on *C. propinquus*.
6. Alpha, Ky., on *C. placidus*.
7. Gainesville, Va., on *C. propinquus*.
8. Dent Co., Mo., on *C. medius*.
9. Highlands, Ala., on *C. rusticus*.
10. Indianapolis, Ind., on *C. rusticus*.
11. Galloway, Mo., on *C. longidigitus*.
12. Mott, N. D., on *C. virilis*.
13. Iowa City, Iowa.
14. Meadville, Pa.

Remarks: These observations have been confirmed by the writer in numerous specimens examined. Especially notable are the elevated major annulations mentioned above, giving a saw-toothed appearance to the margins in total mounts.

Cambarincola (Coronata) philadelphia (Leidy, 1851)

- Astacobdella philadelphia*, Leidy 1851. Proc. Acad. Nat. Sci. Phila. 209.
Astacobdella philadelphia, Verrill 1873. Rep. U.S. Comm. Fish. 688.
Branchiobdella philadelphia, Moore 1894. Proc. Acad. Nat. Sci. Phila. 427-428.
Bdellodrilus philadelphicus, Moore 1895. Jour. Morph. 10:497-498.
Bdellodrilus philadelphicus, Pierantoni 1912. Ann. Mus. Zool. Univ. Napoli, N.S. 3(24).
Cambarincola philadelphia, Ellis 1912. Proc. U.S.N.M. 42:484.
Cambarincola philadelphia, Ellis 1914. Proc. U.S.N.M. 48:190-192.
Cambarincola philadelphia, Ellis 1918. Trans. Amer. Micr. Soc. 37:49-51.
Cambarincola philadelphia, Ellis 1919. Proc. U.S.N.M. 55:260-263.

Description from Ellis 1919:261-263:

"In the original description of this species Leidy gives the following: 'Head campanulate, terminated by a circular or elliptical crenated lip, fringed with very minute stiff hairs; dental plates brown, nearly equal, forming an isosceles triangle, with the base longest and attached, apex of superior plate ending in a sharp conical point with several minute denticulations on each side; apex of inferior plate bifurcated into two points, with two minute denticulations on each side.' From this description the lower jaw may be regarded as a six-toothed jaw, having two large apical teeth and two small teeth on each side. The upper jaw is not so easily understood. The upper jaw bears "x" teeth, if x equals 1 plus Y, in which statement "y" is more than two (*several minute denticulations*, according to Leidy). This interpretation of the upper jaw would give a minimum of seven teeth; that is, one large tooth plus at least three teeth on each side.

"Moore [1894] figures a specimen which he assigns to Leidy's species, having jaws of the dental formula 7-10. The upper jaw as figured has

one large apical tooth, and three small denticles on each side, and the lower jaw has two large teeth, and four small denticles on each side. Moore's figure of the head of this worm shows that the upper lip is composed of four distinct but small lobes, and the lower lip of two large subequal lobes. At the junction of these upper and lower lips on each side is a small intermediate lobe. These six lobes are small enough to fall in Leidy's description of a "circular or elliptical, crenated lip."

"From the examination of a large series of specimens and a study of many living individuals at Douglas Lake, Michigan, the usual dental formula of this species seems to be 5-4. The upper jaw has one large tooth with two small denticles on each side and the lower two large teeth with two small denticles. The variation in the number of teeth figured and described may be accounted for by the fact that the sides of both upper and lower jaws of this species often bear small tubercles below the small denticles—that is, toward the base of the jaw—and these small tubercles could easily be confused with teeth. As understood in this paper, a tooth or denticle is a tubercle on the dental face bearing a distinct tooth cap. These tooth caps are lighter in color than the dental ridge, have 5 definite points and definite form. Two specimens from Tilhance Creek, W. Va., one from Indian Creek, W. Va., and one from Douglas Lake, Michigan, had jaws with more teeth—that is, definite teeth with tooth caps—than the regular 5-4 type, showing that some variation does occur.

"The plurilobate condition of the prostomium is regular and definite, the upper lip having four subequal lobes, the lower, two large, subequal lobes with a small, often inconspicuous lobe present at the junction of the upper and lower lip on each side of the mouth. In the living worms it was observed that the four lobes of the upper lip and to a less extent the two lobes of the lower lip could be extended to form distinct tentacles on the lips. Several specimens from various localities were found in the collections, killed with these tentacles fully extended. Most of the preserved specimens examined showed these tentacles, the lobes of the lips being extended beyond the level of the lips so that the tentacles, although small, were distinct. It was also found that worms of this species could flatten the entire lip, so that the lobes were scarcely visible. Preserved specimens which had been killed with the lips in this flattened condition were separated often with difficulty from individuals of the first group of species of this genus, but close examination in nearly every case showed the regular emarginations marking the location of the lobes of the lips. The lobes were easily seen in a young worm less than three hours old which was examined in water. This worm extended and contracted the lobes in the same manner as an adult. *Cambarincola philadelphica* was the most variable species studied."

Previous locality records:

Leidy 1851:209—

1. Philadelphia, Pa., on *Astacus bartonii*.

Moore 1894:428—

1. Philadelphia, Pa., and Watauga Co., N. C.

Moore 1901:542—

1. From Illinois on *Cambarus diogenes* and *C. blandingii*.

Ellis 1918:50—

1. James Island, Potagannissing Bay, Mich., on *C. virilis*.
2. Pilot Harbor, Sitgreaves Bay, north side of Drummond Island, Potagannissing Bay, Mich., on *C. virilis*.
3. Little Case Island, head of Detour Passage, Mich., on *C. virilis*.
4. Harbor Island, Potagannissing Bay, Mich., on *C. virilis*.

Ellis 1919:260-261—

1. Cheat Bridge, W. Va., on *C. bartonii carinirostris*.
2. Chenoweth Creek, between Beverly and Elkins, W. Va., on *C. bartonii carinirostris*.
3. Laurel Fork of Cheat River, near Seneca Point, W. Va., on *C. bartonii carinirostris*.
4. Right Hand Fork at Queens, W. Va., on *C. obscurus*.
5. Rock House River, near Baileyville, W. Va., on *C. dubius*.
6. Bangers Springs, Hilton, W. Va., on *C. bartonii*.
7. Crane Creek, W. Va., on *C. bartonii veteranus*.
8. Elk River at Cogar's Mill, W. Va., on *C. bartonii*.
9. Cheat River near the Pike, W. Va., on *C. bartonii carinirostris*.
10. Tilhance Creek, Black Creek Valley, W. Va.
11. Indian Creek, tributary of the Elk River in Kanawha County, W. Va., on *C. bartonii veteranus*.
12. Stone Coal Creek between Buckhannon and Weston, W. Va., on *C. obscurus*.
13. War Creek, headwaters of the Big Sandy in McDowell Co., W. Va., on *C. dubius*.
14. Coney Creek, Bainbridge, Pa., on *C. bartonii*.
15. Stony Man Mountain, Va., on *C. bartonii*.
16. North Fork of Blackwater, Courtland, W. Va., on *C. bartonii carinirostris*.
17. Raleigh, N. C., on *C. bartonii acuminatus* and *C. latimanus*.
18. Wytheville, Va., on *C. bartonii*.
19. Scholarie Creek, Green Co., Catskills, N. Y., on *C. bartonii*.
20. Spring Branch, three miles east of Mammoth Cave, Ky., on *C. bartonii tenebrosus*.
21. Left Hand Fork of Middle Fork of Valley, Cassidy, W. Va., on *C. obscurus*.
22. East River, W. Va., on *C. bartonii*.
23. Trubies Sun, W. Va., on *C. obscurus*.
24. Between Paoli and Wyandotte, Ind., on *C. rusticus*.
25. St. Marys River, Ft. Wayne, Ind.
26. Bluffton, Ind., on *C. rusticus*.
27. Rhinelander, Wis., on *C. diogenes*.
28. Maple River, Douglas Lake, Mich., on *C. propinquus* and *C. virilis*.
29. White River, Irondale, Anderson, Ind., on *C. rusticus*.
30. Bloomington, Ind., on *C. Propinquus*.
31. Oxford, Ohio.
32. North Judson, Ind.

New locality records:

1. Alama, Temporal, and Vera Cruz, Mexico, on *C. blandingii acutus*.
2. Oakwood, Ill., on *C. propinquus*.
3. Highland, N. C., on *C. bartonii*.
4. Fargo, N. D., on *C. immunis*.
5. Indianapolis, Ind., on *C. rusticus*.
6. Van Buren, Mo.
7. Green County, Mo., on *C. neglectus*.
8. Wilburton, Okla., on *C. longimonus*.
9. Hidden River, Cave, Hart Co., Ky., on *C. bartonii tenebrosus*.
10. Mad River, Emory, Ohio.
11. Loup Creek, W. Va.
12. Warren Co., Pa.

Remarks: The internal characters of this species omitted by Ellis are well summarized by Leidy in his original description (1851:209):

"Body whitish, translucent; sides nearly parallel, a little broader posteriorly, sixteen alternately broad and narrow segments exclusive of head and posterior end. Head campanulate, terminated by a circular or elliptical crenated lip, fringed with very minute stiff hairs, one two-thousandth of an inch long. Acetabulum circular, one-sixth or one-fourth of a line in diameter; mouth elliptical. Dental plates brown, nearly equal, forming an isosceles triangle, with the base longest and attached apex of superior plate ending in a sharp conical point; with several minute denticulations on each side. Stomach capacious, nearly filling the anterior eight alternately broad and narrow segments posterior to the head. Anus dorsal, one-fifth of a line from the acetabulum. Generative opening ventral, anterior to the anal aperture. Length, one to four lines; breadth, one-sixth to one-half of a line. Head, one-sixth to one-half of a line long."

This species has a wide, short, cylindrical spermatheca. It possesses the characteristics of the genus.

Cambarincola okadai Yamaguchi, 1933, sp. dub.

Cambarincola okadai, Yamaguchi 1933. Proc. Imp. Acad. 9(4):191-193.

Cambarincola okadai, Yamaguchi 1934. Jour. Fac. Sci. Hokkaido Imp. Univ. 3(3):190-191.

Description from Yamaguchi 1933:191-193:

"Recently through the kindness of Prof. Dr. Y. Okada the present writer had an opportunity to examine several specimens of a branchiobdellid worm attached to the sternal surface and appendages of crayfish formerly transferred from America into Lake Chuzenji, Nikko. The specimens were collected by him in 1928 and preserved in formalin. They are undoubtedly referable to the genus *Cambarincola* Ellis 1912, and seem to me to represent a new species, though closely related to the American species, *C. philadelphia* and *C. chirocephala*. . . .

"The preserved specimens are whitish in color and more or less transparent. The body is rather elongate and cylindrical, and in most speci-

mens it slightly curves dorso-ventrally with the ventral side concave. The head is broader than the first trunk segment and is distinctly demarcated from the latter by a constriction. The trunk segments gradually widen from I to VI and then become narrower towards the posterior portion. Among the specimens examined, the largest is 7 mm. long and 0.5 mm. wide at the widest trunk segment. The dorsal part of the peristomium is provided with four distinct sagittiform appendages, while the ventral part is thick and slightly bilobed. The mouth is surrounded by about sixteen circumoral papillae, which are also found in other genera, such as *Ceratodrilus*, *Stephanodrilus*. Both the dorsal and ventral dental plates are slightly brown in color and of similar shape, forming an isosceles triangle with the base longest. Each plate has a large conical tooth forming the apex of the plate, and two small denticles on each side. Unlike *Ceratodrilus* and *Pterodrilus*, the worm is destitute of trunk appendages. The spermathecal pore and the male sexual aperture each open on a slightly elevated papillae in the midventral line in trunk segments V and VI respectively. The oviduct pores are paired, situated on the ventro-lateral sides of trunk segment VII. The anterior nephridia open in a common median dorsal pore on trunk segment III. The digestive tract runs almost straight from the mouth to the anus. Two pharyngeal diverticula, one dorsal and the other ventral, are present. The testes and funnels are paired in trunk segments V and VI; the body cavity of these segments is filled with abundant male reproductive cells in different developmental stages. The spermatheca is tubular and not bifid. The spermathecal vesicle is bifid, having the accessory sperm tube, so named by Ellis (1912).

"Remarks:—The present species has plurilobate peristomium which is present among the genus only in *C. philadelphia*, *C. chirocephala* and *C. homodonta*. [Later placed in the genus *Stephanodrilus* (Yamaguchi 1934:200-201).] Though closely related to *C. philadelphia* and *C. chirocephala* in nearly all characters, is distinguishable from them in the dental plates especially in the ventral plate; according to Ellis (1920), there are two large teeth and two small denticles in *C. philadelphia* and four subequal denticles in *C. chirocephala*, while the new species has a ventral plate provided with a large apical tooth and two small denticles on each side.

"Ellis [1919] pointed out that the primitive type of dental plates in branchiobdellids is probably a subequal five-toothed form. According to him, the type is represented by the formula C-B-C-B-C. Therefore both the dorsal and ventral plates of the new species, provided with a large median tooth are denoted by the formula, c-b-A-b-c. As to the dentation *C. philadelphia* and *C. chirocephala* are similar to the new species in the dorsal plate, but the ventral plate of *C. philadelphia* is shown as c-b-

b-c lacking the large median tooth, and that of *C. chirocephala* is indicated by the formula c-B-B-c showing the disappearance of the median tooth and the increase in size of the inner pair. From the difference of the dentition in the ventral plate, it seems to the writer to be right to recognize the Japanese worm as distinct from *C. philadelphia* and *C. chirocephala*.

"So far as the writer knows, there has been no report on crayfishes from Lake Chuzenji and adjacent districts except these newly transferred from America. The present species was probably introduced from America together with the American crayfish. However it is very noticeable that the present species and *C. homodonta* [Later placed in genus *Stephanodrilus* (Yamaguchi, 1934:200-201)], both occurring in Japan, have the dentition of the *homodonta*-type, while in all species belonging to the genus hitherto found in America the dorsal and the ventral plates are different in dentition."

Remarks: This species appears to the writer to be identical with *Cambarincola philadelphica*, as it differs from it only in the dentition of the lower jaw, and *C. philadelphica* is an extremely variable form, as outlined above.

GENUS XIRONOGITON Ellis, 1919

Branchiobdella (in part), Moore 1894. Proc. Acad. Nat. Sci. Phila. 425-427.

Bdellodrilus (in part), Pierantoni 1912. Ann. Mus. Zool. Univ. Napoli, N.S. 3(24).

Xironogiton, Ellis 1919. Proc. U.S.N.M. 55:247-248.

Xironogiton, Stephenson 1930:802.

With the characteristics of the subfamily; spermatheca simple, not bifid; each nephridium of the anterior pair opening to the outside through a separate pore in the dorsal half of segment III; a distinct accessory sperm tube present in segment VI; body distinctly depressed; posterior segments wider and flatter than the anterior segments; posterior sucker ventral; segment IX much reduced so body appears to be composed of eight or fewer segments; alimentary canal looped once or twice in segment VII.

Type species: *Xironogiton instabilis oregonensis* Ellis, 1919.

KEY TO THE SPECIES OF THE GENUS XIRONOGITON

1. (a) Glandular concave disks near the lateral margin of the ventral surface of segments VIII and IX; body usually spatula-shaped.....
.....*Xironogiton occidentalis* Ellis, 1919
- (b) No conspicuous glandular disks near the lateral margin of the ventral surface of segments VIII and IX; body usually flask-shaped..... 2
2. (a) Two teeth of the longest pair in the upper jaw separated by but one tooth; if two long teeth are contiguous the inner one is the longer.....
.....*Xironogiton instabilis instabilis* (Moore, 1894)
- (b) Two teeth of the longest pair in the upper jaw separated by two teeth; if two long teeth are contiguous the outer one is usually the longer.....
.....*Xironogiton instabilis oregonensis* Ellis, 1919

Xironogiton occidentalis Ellis, 1919*Xironogiton occidentalis*, Ellis 1919. Proc. U.S.N.M. 55:248-249.

Description from Ellis 1919:248-249:

"Body segments elongate and distinctly depressed; body segments I to VIII distinct, each slightly constricted at its anterior and posterior ends giving the segmental junctions sharp definition; segment IX greatly reduced so that the body appears to be composed of but eight segments; segments expanding gradually and regularly in width to segment VII, which is the widest body segment; segment XIII almost as wide as segment VII; segments IX and X so narrow and inconspicuous that the caudal sucker appears to be inserted under the posterior half of segment VIII; head large, its anterior third defined by a groove; lips two, each with a slight median emargination, otherwise entire; a few short transparent bristles on the margins of the lips; major pharyngeal diverticula three, two dorsal and one ventral; the ventral diverticulum about midway between the levels of the two dorsal diverticula; dental formula 6-6 . . . but with the two teeth of the "a" order unequal in size; tooth plan of upper jaw C-B-a-a-B-C, teeth of the "C" order being slightly smaller than those of the "B" order but larger than those of the "a" order, the two "a" teeth unequal; difference in size of teeth slight so that the jaws approach the subequal-toothed jaw type; anterior nephridia alternating in segments II and III, opening to the outside through separate pores on the dorso-lateral surface of segment III; spermatheca simple; testes present in segments V and VI; vasa deferentia from segments V and VI joining the atrium in segment VI; a long accessory sperm tube present; alimentary canal not conspicuously expanded in the first three segments, wider in segment IV, increasing in diameter in segments V and VI, narrowing in segment VII, in which segment the intestine forms a more or less definite "s"-shaped curve; intestine narrowing rapidly in the anterior half of segment VIII and continuing as a somewhat crooked tube to the anal opening on the dorsal surface of the posterior half of segment IX: because of the reduced condition of the segment IX, the anal opening is subterminal; adhesive disks on segment XIII prominent, those on segment IX inconspicuous.

"The two specimens from which this species was described measured 4.5 and 5 mm., respectively. *X. occidentalis* resembles a large, much extended specimen of *X. instabilis* (Moore). It is easily separated from that species by the glandular disks on the ventral surface of segments VIII and IX and by the distinct segmental junctions."

Type: U.S.N.M. No. 17639 from Crab Creek, Wash., on *Astacus klamathensis*. Length 4.5 mm.

Previous locality records:—

Ellis 1919:248—

1. Crab Creek, Wash., on *Astacus klamathensis*.

New locality records:

1. Vernonia, Ore., on *A. trowbridgii*.
2. Harney Co., Ore., on *A. gambelii*.
3. Young River, Ore., on *A. klamathensis*.

Remarks: The additional material studied agreed with the above description except in regard to size, as worms were found which were 6.0 mm. long, distinctly larger than any Ellis studied.

Xironogiton instabilus instabilus (Moore, 1894)

Branchiobdella instabilia, Moore 1894. Proc. Acad. Nat. Sci. Phila. 425-427.

Branchiobdella instabilia, Smallwood 1906. Biol. Bull. Woods Hole, 11:100-111.

Branchiobdella instabilia, Ellis 1912. Proc. U.S.N.M. 42:484

Bdellodrilus instabilus, Pierantoni 1912. Ann. Mus. Zool. Univ. Napoli, N.S. 3(24).

Bdellodrilus instabilus, Hall 1914. Proc. U.S.N.M. 48:190.

Xironogiton instabilus, Ellis 1919. Proc. U.S.N.M. 55:252-253.

Description from Moore 1894:425-427:

"Body in a state of contraction very short and stout, the posterior four segments forming a flattened disk-shaped expansion which is scarcely longer than broad; the first four body segments are much more narrow, but increase somewhat in breadth to the fourth, posterior to which the increase is very rapid to the seventh; the eighth is slightly narrower and develops lateral wing-like flaps, which, sloping ventralward, bound a decided ventral concavity in this region; posteriorly they embrace the sucker-bearing segments. The head and anterior segments are terets. Under normal conditions the large head is considerably broader than the following segments, which form a neck-like constriction, to which the head is attached by a very mobile fold, forming a distinct annulus. The emarginated lips are slightly crenulated, and form an almost continuous muscular thickening around the mouth. The postoral constriction is well-marked, but not so deep as in *B. pulcherrima*. Numerous short stiff hairs fringe the lips and head, and in young individuals are present on the body segments also.

"The dark brown jaws are provided with four strong curved conical teeth, which diverge slightly; the outer pair are symmetrical, the left tooth of the middle pair is much larger than the right; this being the case in both jaws in nearly all of the many specimens examined.

"The acetabulum resembles that of *B. pulcherrima* in being directed ventralward. Its diameter is greater than that of the first or second body segments. Bi-annulation is conspicuous on the anterior four post-cephalic segments only.

"The alimentary canal is strongly sacculated in the fourth and fifth segments, in the sixth is pushed to the left side by the development of the atrium (this occurs in adults only), in the seventh is thrown into a complete double transverse loop which passes first to the right and then

to the left, and finally passes directly to the anus in the ninth body segment. The spermatheca is very small and inconspicuous, while the penis-sac is well developed, and possesses a long vermiform appendage (atrium) which forms a loop dorsally over and around the intestine. Sexual and nephridial openings as in *B. pulcherrima*.

"In contraction the body of this species is shaped like a short-handled racket; in extension it has the outline of an Indian club from dorsal and ventral views.

Length of mature animal.....	5.5 mm.
Maximum breadth.....	1.3 mm.
Diameter of acetabulum.....	.5 mm.
Transverse diameter of jaw.....	.048 mm.
Length of cocoon without pedicle.....	.35 mm.

"The cocoons resemble those of the last described species, but are frequently provided with an apical fibrous tuft. They are invariably attached (to the extent of my experience) to the palmar surface of the propodite of the great chelae. The animals themselves are largely restricted in their distribution to the same segments of the limb, and are usually to be found in numbers clustered at the base of the pincers to which position the form of the body peculiarly adapts them; for while the constricted anterior region, by reason of its tenuity, easily escapes crushing between the closing limbs of the chela, in which position it is frequently liable to be caught, the important organs of reproduction and digestion are massed together near the base of attachment, entirely out of reach of danger from this source. Frequently they wander to other parts of the same pair of limbs, or even to the two pairs of ambulatory limbs following."

Type: From Watauga Co., N. C., and Delaware Co., Pa.

Previous locality records:

Moore 1894:427—

1. Watauga Co., N. C., and Delaware Co., Pa.

Smallwood 1906:100—

1. Lake Clear, Franklin Co., N. Y.

Ellis 1919:252—

1. Stony Man Mountain, Va., on *Cambarus bartonii*.
2. West Branch of Clenmark Creek, North Rose, N. Y., on *C. bartonii robustus*.
3. Trubies Run, a tributary of the Buckhannon River, 7 miles above Buckhannon, W. Va., on *C. obscurus*.
4. Blowing Rock, Watauga Co., N. C., on *C. bartonii*.
5. Chenoweth Creek between Beverly and Elkins, W. Va., on *C. bartonii carinirostris*.
6. Cheat River Bridge, Randolph Co., W. Va., on *C. bartonii carinirostris*.
7. Right Hand Fork of Chenoweth Creek, a tributary of the Cheat River, Queens, W. Va., on *C. obscurus*.
8. Elk River at Cogars Mill, W. Va., on *C. bartonii* subspecies.
9. Cheat River, near the Pike, W. Va., on *C. bartonii carinirostris*.

New locality records:

1. Cleveland, N. Y.
2. Jackson Run, Warren Co., Pa.

Remarks: Moore adequately describes the material studied, which did not present much variation.

Xironogiton instabilis oregonensis Ellis, 1919

Xironogiton oregonensis, Ellis 1919. Proc. U.S.N.M. 55:249-251.

Xironogiton oregonensis oregonensis, Ellis 1919. Proc. U.S.N.M. 55:254.

Xironogiton oregonensis pectinatus, Ellis 1919. Proc. U.S.N.M. 55:251.

Description from Ellis 1919:249-251:

"Body distinctly depressed, general outline of contracted specimens racket- or flask-shaped, extended specimens conspicuously wider in the posterior half of the body than in the anterior; head and body segments I and II subequal and subterete; segment IV distinctly wider than segment III and somewhat depressed; segments V to VIII conspicuously wider than the anterior portion of the body, rather completely fused at the segmental junctions so that the segmental junctions are not clearly defined as they are in the anterior four segments; maximum width of the body in segment VII; segments V and VIII subequal; segmental margins of segments V to VIII broadly flattened forming a conspicuous shelf beyond the thicker portion of the body; segment IX greatly reduced, not prominent in dorsal view; caudal sucker large, ventral, its width in contracted specimens about equal to that of the head; head large, in contracted specimens exceeding the first two body segments in size; head divided into two rather distinct units, the anterior being slightly shorter than the posterior; lips two, each with a median emargination; dental formula 5-4 or 6-5, varying from 4-4 to 7-6 . . . major pharyngeal diverticula three, two dorsal and one ventral; each anterior nephridium opening to the outside through a separate pore in segment III; spermatheca in segment V, small and simple, subglobose with a small dorsal tubular portion, not bifid; testes in segments V and VI; vasa deferentia from segments V and VI joining the large atrium in segment VI; accessory sperm tube present and well-developed; alimentary canal rather straight in segments I to V, maximum enlargement in segment V, intestine more or less displaced (usually to the right) in segment VI depending upon the state of the enlargement of the reproductive organs in that segment; intestine forming two rather distinct loops in segment VII, decreasing rapidly in diameter from segment VII to the anal opening on the dorsal surface of segment IX; largest specimens examined was strongly contracted and measured 2.0 mm. in length."

Type: U.S.N.M. No. 17639 from Eugene, Ore., on *Astacus klamathensis* Stimpson.

Previous locality records:

Ellis 1919:249-251—

1. Eugene, Ore., on *Astacus klamathensis*.
2. Sequallitchew Lake, Pierce Co., Wash.

New locality records:

1. 22 miles from Vintage, Wash., on *A. sp.*
2. Klamath, Ore., on *A. trowbridgii*.
3. Deer Creek, Ore., on *A. trowbridgii*.
4. Bovill, Idaho, on *A. gambelii*.
5. St. Helens, Ore., on *A. trowbridgii*.
6. Lewis County, Wash., on *A. trowbridgii*.
7. Redmond, Wash., on *A. trowbridgii*.
8. Centralia, Wash., on *A. trowbridgii*.
9. Vernonia, Ore., on *A. trowbridgii*.
10. Harney Co., Ore., on *A. gambelii*.
11. Evanston (Bear River), Wyo., on *A. gambelii*.

Remarks: Ellis believed this form to be a distinct species on the basis of the tooth differences as outlined above. However, additional material has shown considerable overlap in tooth formula and so the present writer believing this worm to be a western subspecies of the eastern form described by Moore, here presents *Xironogiton oregonensis* as a subspecies under the name *Xironogiton instabilis oregonensis*.

GENUS XIRONODRILUS Ellis, 1919

Branchiobdella (in part), Moore 1894. Proc. Acad. Nat. Sci. Phila. 423-425.
Bdellodrilus (in part), Pierantoni 1912. Ann. Mus. Zool. Univ. Napoli, N.S. 3(24).
Xironodrilus, Ellis 1919. Proc. U.S.N.M. 55:243-244.
Xironodrilus, Stephenson 1930:802.

With the characteristics of the subfamily; spermatheca simple, not bifid; no accessory sperm tube; each nephridium of the anterior pair opening to the outside through a separate pore in the dorsal half of segment III; body depressed; caudal sucker ventral; at least nine segments visible in dorsal view; a glandular concave disk near each lateral margin of the ventral surface of segments VIII and IX; segments I to IX distinct; alimentary canal straight.

Type species: *Xironodrilus formosus* Ellis, 1919.

KEY TO THE SPECIES OF THE GENUS XIRONODRILUS

1. (a) Middle tooth of the upper jaw the longest tooth if teeth are odd in number; if teeth are even in number, the middle pair is the longest*Xironodrilus formosus* Ellis, 1919
- (b) Middle tooth of the upper jaw shorter than either of the two teeth adjoining it.....2
2. (a) Dental formula 3-3.....*Xironodrilus pulcherrimus pulcherrimus* (Moore, 1894)
- (b) Dental formula varying from 4-4 to 5-5.....*Xironodrilus pulcherrimus dentatus* new subspecies

Xironodrilus formosus Ellis, 1919

Xironodrilus formosus, Ellis 1918. Trans. Amer. Micr. Soc. 37:49-51.

Xironodrilus formosus, Ellis 1919. Proc. U.S.N.M. 55:244-245.

Description from Ellis 1919:244-245:

"Body rather elongate and distinctly depressed; width of the head approximately equal to that of segment I and less than that of segment II; body segments increasing in width regularly from segment I to segment VII; segment VII usually the widest segment of the body (In strongly contracted specimens and in specimens in which segment VII is not distended with sex cells, segments VII and VIII are usually about the same width, or segment VIII may be slightly wider than segment VII); nine body segments distinct and easily seen in the dorsal view; each segment slightly constricted anteriorly and posteriorly so that the junctions of the segments are evident; segments narrowing regularly and rapidly from the middle of segment VIII to the caudal sucker; diameter of caudal sucker less than or barely equal to the width of the head; head subcylindrical, its anterior third defined by a groove or constriction; lips two, the upper slightly longer than the lower; both upper and lower lips with small but rather definite median emargination, otherwise entire; margins of the lips bearing a few short, transparent bristles; tooth formula usually 5-4 or 5-5, varying from 4-3 to 6-5; . . . tooth plan of both jaws c-B-A-B-c, upper jaw sometimes c-B-A-B-c-d; width of lower jaw 24 micra (in worm 1.4 mm. body length) to 30 micra (in worm 2.8 mm. body length) major pharyngeal diverticula three, two dorsal and one ventral, the ventral diverticulum about midway between the levels of the two dorsal diverticula; anterior nephridia alternating in segments II and III (of 44 specimens examined on this point 25 had the nephridium in segment II on the right side and that in segment III on the left; 17 had the nephridium in segment II on the left side and that in segment III on the right; and two individuals had both nephridia in segment II); anterior nephridia opening to the outside through separate pores on the dorsolateral surface of segment III; spermatheca in segment V, composed of three parts, a short muscular portion near the spermathecal pore, a middle tubular portion and a dorso-posterior, globose portion; testes in segments V and VI; vasa deferentia from segments V and VI joining the atrium in segment VI; no accessory sperm tube; alimentary canal straight, passing through the body near or along the mesial axis, somewhat expanded in segments I and II, strongly sacculated in segments III and IV, much narrowed in segments V and VI, slightly expanded in segment VII, narrowing from segment VII to the anal opening on the dorsal surface of the anterior half of segment X (In surface view the anus appears to open in the posterior half of segment IX, but sagittal sections show that the anal opening is between segments

IX and X and that the rectal portion of the alimentary canal is carried by segment X); caudal sucker ventral; smallest specimen examined 0.8 mm. in length; largest 3.1 mm. (preserved specimens)."

Type: U.S.N.M. No. 17626 from White River, Irondale, near Andersonville, Ind., on *Cambarus rusticus* (Girard). Length 2.7 mm.

Previous locality records:

Ellis 1918:50—

1. James Island, Potagannissing Bay, Mich.
2. Three miles up Potagannissing River, Drummond Island, Potagannissing Bay, Mich.
3. Pilot Harbor, Sitgreaves Bay, North side of Drummond Island, Potagannissing Bay, Mich.
4. Little Cass Island, head of Detour Passage, Mich.
5. Churchville Point, head of Lake George, 46° 31' N, Mich.
6. Harbor Island, Potagannissing Bay, Mich.
7. Winona Slips, Bay City, Saginaw Bay, Mich.

Ellis 1919:244—

1. White River, Irondale, near Anderson, Ind., on *Cambarus rusticus*.
2. White River, Noblesville, Ind., on *C. rusticus*.
3. Lake Michigan, Charlevoix, Mich., on *C. propinquus*.
4. Wabash River, Vincennes, Ind., on *C. propinquus*.
5. Between Paoli and Wyandotte, Ind., on *C. rusticus*.

New locality records:

1. Champaign County, Ill., on *C. virilis*.
2. Indianapolis, Ind., on *C. rusticus*.
3. Patosi, Mo., on *C. medius* and *C. punctimanus*.
4. Huron Co., Mich., on *C. immunis*.
5. Galloway, Mo., on *C. longidigitus*.
6. Emette Co., Mich., on *C. propinquus*.
7. Green Co., Mo., on *C. neglectus*.
8. Ozark, Mo., from Smallen Cave on *C. setosus* (cave crayfish).
9. Iron Co., Mo., on *C. luteus*.
10. St. Francis Co., Mo., on *C. punctimanus*.

Remarks: A large series of this form has been examined and all agree closely with the above description, the teeth variations all falling within the limits outlined above.

Xironodrilus pulcherrimus (Moore, 1894)

Branchiobdella pulcherrima, Moore 1894. Proc. Acad. Nat. Sci. Phila. 423-425.

Branchiobdella pulcherrima, Smallwood 1906. Biol. Bull. Woods Hole, 11:100-111.

Branchiobdella pulcherrima, Ellis, 1912. Proc. U.S.N.M. 42:484.

Bdellodrilus pulcherrima, Pierantoni 1912. Ann. Mus. Zool. Univ. Napoli, N.S. 3(24):1-28.

Bdellodrilus pulcherrima, Pierantoni, 1912. Ann. Mus. Zool. Univ. Napoli, N.S. 3(24).

Bdellodrilus pulcherrimus, Hall 1914. Proc. U.S.N.M., 48:190.

Xironodrilus pulcherrimus, Ellis 1919. Proc. U.S.N.M. 55:246-247.

Description from Moore 1894:423-425:

"The beautiful transparency of the anterior segments which enables one to see with great distinctness the internal organs of that region suggested the name given to this species.

"Form rather stout, the body depressed, especially in the posterior

region. The segments increase regularly in width to the seventh, which is the broadest; and behind which they rapidly narrow to the acetabulum. Each post-cephalic segment consists of an anterior larger and a posterior smaller annulus. The ventral surfaces of the eighth and ninth segments are strongly flattened, and each bears on its extreme lateral margins a cup-shaped adhesive organ, into the central depression of which a conspicuous gland opens. These are directed ventralward and doubtless serve as accessory organs of attachment to aid the rather weak sucker. Those on the eighth segment are usually the larger, but a considerable range of variation is exhibited in this respect. The structures become proportionally larger and more conspicuous in older individuals.

"The head is urn-shaped, slightly longer than broad in preserved specimens, and its greatest width less than or just equal to that of the first body segment. The breadth of the head varies greatly with the degree of contraction of the specimen, but in the living individual always appears narrow, and to form part of the generally even tapering outlines of the body, never abruptly expanded as in *B. instabilis*. The oral region is separated from the cephalic region by a deep constriction, which completely encircles the head. The mouth is enveloped by a pair (dorsal and ventral) of distinct thick muscular lips, of which the dorsal one is the larger and droops downward, partially enclosing the ventral lip. Each presents a slight median emargination, but is otherwise entire. The lips and head, as well as the sides of the principal annuli of the body, are provided with a fringe of delicate hairs. Mouth opening nearly circular, between the parted lips.

"The jaws are small and inconspicuous, in adult specimens less than one-twelfth of the width of the head, and of a pale brown or amber color. The rounded base bears three teeth, of which the larger lateral ones are stout, curved, and divergent, while the smaller median one is straight and sharp-pointed. The variations in the jaws involve frequent unsymmetrical development of the teeth. The dorsal and ventral jaws are similar, and both are fixed opposite to the constriction behind the lips, the teeth being directed inward.

"The straight alimentary canal is strongly sacculated in the second, third and fourth segments, behind which it is narrow, and direct in its course to the anus, which opens on a slight papilla on the dorsal side of the ninth segment.

"The greater part of the body cavity of the fifth and sixth segments is filled with testicular cells in various stages of development; and the glandular thickening of the skin of these segments renders the walls conspicuously opaque. The two pairs of vasa deferentia open into the nearly spherical atrium in the sixth segment. A conspicuous and broadly pyriform spermatheca opens on the fifth segment. The ovaries and

accessory structures occupy the seventh. The anterior nephridia alternate in position, but open to the exterior by paired orifices in segment three. The posterior paired nephridia occupy the space on each side of the intestine in segment eight.

"This species is colorless and more or less translucent; the first four segments behind the head are remarkably clear and translucent, but behind this the body walls are rather opaque and the position of the internal organs obscured. The alimentary canal is throughout darkly colored, except within the head.

"Blood very pale red.

Length of mature individuals.....	6 mm.
Maximum breadth.....	1.3 mm.
Width of jaws.....	.06 mm.
Diameter of acetabulum.....	.6 mm.

"Cocoons of this species are almost spherical and are borne on short stout stalks. Usually they are attached to the broad surfaces of the body, i.e., the sides of the carapace, inner faces of the anterior abdominal epimere, and the sternal face of the tail fin.

"Length of cocoon without stalk 46 mm.

"The adults are found attached almost anywhere on the exterior of the crayfish but more especially on the tergal surface."

Type: From Watauga Co., N. C., on *Cambarus bartonii*.

Previous locality records:

Moore 1894:425—

1. Watauga Co., N. C., on *Cambarus bartonii*.

Smallwood 1906:110—

1. Lake Clear, Franklin Co., N. Y.

Ellis 1919:246—

1. Trubies Run, a tributary of Buckhannon River, 7 miles above Buckhannon, W. Va., on *C. obscurus*.
2. Right Hand Fork of Chenoweth Creek, Queens, W. Va., on *C. obscurus*.
3. Shavers Fork, of Cheat River, W. Va., on *C. bartonii carinirostris*.
4. Cheat River, near the Pike, W. Va., on *C. bartonii carinirostris*.
5. Cheat River Bridge, Randolph County, W. Va., on *C. bartonii carinirostris*.
6. Chenoweth Creek, between Beverly and Elkins, W. Va., on *C. bartonii carinirostris*.
7. Laurel Fork, Cheat River, near Seneca Point, W. Va., on *C. bartonii carinirostris*.
8. Indian Creek, Ranawha County, W. Va., on *C. dubius*.
9. Near Baileysville, W. Va., on *C. dubius*.
10. Blowing Rock, Watauga Co., N. C., on *C. bartonii*.
11. Rock House River, near Baileysville, W. Va., on *C. dubius*.

New locality records:

1. Highlands, N. C., on *C. bartonii*.
2. Wilburton, Oklahoma, on *C. longimanus*.

Remarks: This description adequately describes all individuals examined with the exception of the tooth formula, which has greater varia-

tion than Moore realized. The first person to recognize this was Ellis (1919:247) who found that while the North Carolina material had the 3-3 tooth formula of Moore's description, the thirty-seven West Virginia worms had a formula varying from 4-4 to 5-5 with most individuals having a 5-4 formula. On the basis of this Ellis suggested that two subspecies might be represented but did not have enough material to be certain. The present writer has examined material from Highlands, North Carolina, and found the same 3-3 formula of Moore, but on the Oklahoma material the tooth formula was found to be 5-4 and 5-5. On this evidence the writer feels certain that two subspecies are actually represented, and he proposes the following names: *Xironodrilus pulcherrimus pulcherrimus* (Moore, 1894) for the North Carolina worms with the 3-3 formula; and *Xironodrilus pulcherrimus dentatus* new subspecies for the form with the higher tooth formula as outlined above.

GENUS BDELLODRILUS Moore, 1895

Branchiobdella (in part), Moore 1894. Proc. Acad. Nat. Sci. Phila. 421-423.

Bdellodrilus (in part), Moore 1895b. Jour. Morph. 10:497-540.

Bdellodrilus (in part), Pierantoni 1912. Ann. Mus. Zool. Univ. Napoli, N.S. 3(24).

Bdellodrilus, Stephenson 1930:801.

With the characteristics of the subfamily; spermatheca bifid; anterior nephridia opening to the outside through a single pore in the mid-dorsal line of segment III; no accessory sperm tube; a pair of clear large glands present in each of the nine postcephalic segments; no trunk appendages; penis eversible.

Type and only species: *Bdellodrilus illuminatus* (Moore, 1894).

Bdellodrilus illuminatus (Moore, 1894)

Branchiobdella illuminata, Moore 1894. Proc. Acad. Nat. Sci. Phila. 421-423.

Bdellodrilus illuminatus, Moore 1895b. Jour. Morph. 10:497-540.

Bdellodrilus illuminatus, Pierantoni 1912. Ann. Mus. Zool. Univ. Napoli, N.S. 3(24).

Bdellodrilus illuminatus, Ellis 1912. Proc. U.S.N.M. 42:485.

Bdellodrilus illuminatus, Hall 1914. Proc. U.S.N.M. 48:190-192.

Description from Moore 1894:421-423:

"Body very slender in complete extension, but robust in contraction; tapering from the seventh segment very gently toward the head, and suddenly to the posterior sucker; terete in transverse section in all regions. Bi-annulation of segments very conspicuous throughout the entire length. Posterior sucker small and weak, on the same axis as the body segment. Head small, slender, and elongated; the post-oral part distinctly bi-annulate. Lips long and weak, of nearly equal size; ridged within by longitudinal folds. Mouth opening with its longest diameter transverse. No circumoral or other hairs have been detected in the adults of this species,

and in the young a single small bunch in the median region of each lip is all that is present.

"The jaws are remarkable, and although large, are inconspicuous on account of their transparency and lack of color. On the dorsal one, which is much the larger, a high median ridge is developed, which bears three strong teeth, the points of which are directed posteriorly (down the throat). The ventral jaw is shaped like a U each limb of which is bent out of the common plane into a boomerang shape. The angle of the boomerang on each side is uppermost and bears a very strong curved tooth, the two bounding a deep groove which accommodates the dorsal dentigerous ridge.

"The stomach is comparatively small, and behind it the evenly tubular intestine is thrown into loops, which become more obvious with the greater degree of contraction of the animal.

"In connection with the vascular system is developed a remarkable shallow sinus which covers almost the entire surface of the alimentary canal. This presents dorsal and ventral longitudinal enlargements into which the principal vascular trunks are received. The extensive vascular surface with the contained bright red blood thus presented gives the animals a delicate pinkish hue which distinguishes living individuals at a glance from the other species herein described.

"In each of the nine post-cephalic segments is a pair of peculiar translucent glandular bodies composed of large nucleated cells, and communicating with the exterior by slender ducts having ventro-lateral openings.

"The anterior two nephridia open into a gourd-shaped vesicle having an opening to the exterior in the mid-dorsal region of the major annulus of the third segment. The spermatheca is short, cylindrical and bifid; the penis-sac short-pediced and spherical, and the atrium clavate and curved. The spermatheca, penis, ovaries, posterior paired nephridia and anus open respectively on the fifth, sixth, seventh, eighth, and ninth post-cephalic segments. Length of full grown individuals, 4 mm., maximum diameter (7th segment) 9 mm., diameter of acetabulum .35 mm."

Type: From Philadelphia, Pa., and Watauga Co., N. C., on *Cambarus bartonii*.

Previous locality records:

Moore 1894:421-423—

1. Philadelphia, Pa., and Watauga Co., N. C., on *Cambarus bartonii*.

Allen 1933:119—

1. Durham, N. C.

New locality records:

1. Macoupin Co., Ill., on *C. virilis*.

2. Champaign Co., Ill., on *C. blandingii acutus*, *C. virilis*.

Remarks: This is an adequate description for the Illinois material examined.

GENUS STEPHANODRILUS Pierantoni, 1906

Stephanodrilus, Pierantoni 1906b. Ann. Mus. Zool. Univ. Napoli, N.S. 2(11).

Stephanodrilus, Pierantoni 1912. Ann. Mus. Zool. Univ. Napoli, N.S. 3(24).

Stephanodrilus, Stephenson 1930:801.

Carcinodrilus, Yamaguchi 1932b. Jour. Fac. Sci. Hokkaido Imp. Univ. 2(1):61-67.

Cambarincola, Yamaguchi 1932c. Proc. Imp. Acad. 8:454-456.

Stephanodrilus (*Stephanodrilus*), Yamaguchi 1934. Jour. Fac. Sci. Hokkaido Imp. Univ. 3(3):191-210.

With the characteristics of the subfamily; spermatheca simple, not bifid; no accessory sperm tube; anterior nephridia opening to the outside through separate pores in the dorsal half of segment III (except in *St. koreanus*); body cylindrical, not depressed, without body appendages.

Type species: *Stephanodrilus sapporensis* Pierantoni, 1906, from Japan.

Only known American species: *Stephanodrilus obscurus* new species.

Stephanodrilus obscurus new species

(Pl. I, Fig. 2; Pl. II, Fig. 6)

Description:

Length of worms examined varied from 2.0 mm. to 3.0 mm. Head subcylindrical, divided into three subequal portions by two constrictions; lips two, dorsal slightly longer than ventral, both entire but may have slightly wavy margin; dorsal and ventral jaws about 30 microns in diameter in a worm 2.5 mm. in length; dental formula 5-5 or 6-6 in material examined; dorsal jaw with the two outer teeth longer than median ones; ventral jaw similar to dorsal. Dorsal jaw may have a small denticle on the outer side of the two longer teeth.

Head diameter greater than segment I, about the same as segment II; segments increase regularly in diameter to segment VI or VII which is about 0.7 mm. in a worm 2.5 mm. long; diameter decreases to caudal sucker which is not especially large; major annulations of segments II to VII distinctly and visibly elevated over minor annulations. Gut relatively straight with sacculations in segments IV and VII.

Testes in V and VI, with a large male bursa in VI nearly filling the segment; spermatheca present in segment V, simple not bifid, enlarged in ventral portion. Anterior nephridia opening to the outside through separate pores in the dorsal half of segment III.

Holotype: From Fall River, Shasta County, California, on *Astacus nigrescens*.

Paratypes: From Fall River, Shasta County, California, on *Astacus nigrescens*.

Remarks: This is the first time this genus has been reported outside of the Japanese region and shows the close relation between the Oriental and Pacific-American faunas. This species differs from the previously described ones in the structure of the jaws and in the entire lips. All

other known forms of this genus have a peristomium divided into lobes which may be extended as digitiform appendages and have jaws provided with at least seven teeth. However these characters have been shown to be specific and not generic for other genera, and since this species otherwise agrees closely with the described forms of *Stephanodrilus* the writer feels that it is a member of that genus.

The holotype will be deposited in the United States National Museum and the paratypes in the collection of Dr. H. J. Van Cleave, of the University of Illinois, and in the collection of the writer.

GENUS TRIANNULATA new genus

With the characteristics of the subfamily; spermatheca simple not bifid; no accessory sperm tube; body cylindrical not flattened; head roughly triangular in shape with protruding lips; major annuli of most segments redivided to give the appearance of three annuli per segment; this is especially evident in the median segments and in moderately contracted specimens; anterior nephridia opening to the outside through separate pores in the dorsal half of segment III.

Type species: *Triannulata magna* new species.

KEY TO THE SPECIES OF THE GENUS TRIANNULATA

1. Lips entire except for a slight median emargination.....
.....*Triannulata magna* new species
2. Lips divided into lobes.....*Triannulata montana* new species

Triannulata magna new species

(Pl. I, Fig. 4; Pl. II, Fig. 8)

Description:

Relatively large worms varying from 5.0 to 8.0 mm. in formalin fixed specimens. Head distinct from body, rounded, roughly triangular; lips two, dorsal slightly longer than ventral which has a slight median notch; lips narrower than head, so have a protruded appearance in side view; dorsal and ventral jaws similar, large, being 250 micra wide in a worm 5.0 mm. long, appearing as triangular blocks of chitin with a tooth at the apex, sides of the triangle not smooth but slightly undulating without definite teeth.

Head distinctly wider than segments I and II, about the same as segment III; segments distinct, increasing in width to segment VI or VII which is about 1.0 mm. in diameter in a worm 5.0 mm. long; segments then decreasing in diameter to the caudal sucker, which is large and prominent with large distinct glands; major annulations of most segments secondarily divided as discussed for genus; intestine relatively straight with sacculations in segments IV and VII.

Testes located in segments V and VI with rounded bursa in VI; spermatheca in V simple not bifid; anterior nephridia opening to the outside through separate pores in the dorsal half of segment III.

Holotype: From Naches, Wash., on *Astacus* sp.

Paratypes: From Naches, Wash., and Redmond, Wash., on *Astacus* sp.

Additional material: From St. Helens, Ore.; Cestsajo, Ore., on *Astacus trowbridgii*; Vernonia, Ore., on *A. klamanthensis*; Rogue River, Ore., on *A. klamanthensis*.

Remarks: This species differs from *Triannulata montana* in the presence of entire lips and untoothed jaws while *T. montana* has lobed lips and toothed jaws.

The holotype will be deposited in the United States National Museum and the paratypes in the collection of Dr. H. J. Van Cleave, of the University of Illinois, and in the collection of the writer.

Triannulata montana new species

(Pl. I, Fig. 1; Pl. II, Fig. 7)

Description:

Body cylindrical and relatively large, up to 5.0 mm. in the material examined; major annuli secondarily divided as described above, head large and distinct; peristomium divided into twelve lobes (four dorsal, four ventral, and four lateral) which may be extended into tentacular appendages, dorsal longer than ventral or lateral; jaws large, 250 micra in diameter in a worm 5.0 mm. long; jaws with a dental formula of 7-5, each with a longer median tooth and smaller lateral ones; head diameter greater than segment I or II, about the same as segment III; segments increasing slightly to segment VI or VII which are about 1.25 mm. in diameter in a worm 5.0 mm. long; segments then decreasing to the caudal sucker which is fairly prominent with well developed glands; segments distinct; intestine relatively straight with sacculations in segments IV and VII.

Testes present in segments V and VI with bursa in VI; spermatheca in segment V simple not bifid; anterior nephridia opening to the outside through separate pores in the dorsal half of segment III.

Holotype: From Kalami River, Wash., on *Astacus* sp.

Paratypes: From North Fork of the Clearwater River near Bovill, Idaho, and from the Kalami River, Wash., between Centralia and Chihalis, on *Astacus* sp.

Remarks: This species is very similar in appearance to *Triannulata magna* but differs greatly in the structure of the jaws and in the lobed peristomium. *Triannulata montana* has toothed jaws while *T. magna* has untoothed jaws; *T. magna* has entire lips rather than the lobed lips of *T. montana*.

The holotype will be deposited in the United States National Museum and the paratypes in the collection of Dr. H. J. Van Cleave, of the University of Illinois, and in the collection of the writer.

GENUS PTERODRILUS Moore, 1895

Pterodrilus, Moore 1895a. Proc. Acad. Nat. Sci. Phila. 449-454.

Pterodrilus, Pierantoni 1912. Ann. Mus. Zool. Univ. Napoli, N.S. 3(24).

Pterodrilus, Ellis 1919. Proc. U.S.N.M. 55:252-255.

Pterodrilus, Stephenson 1930:801.

With the characteristics of the subfamily; spermatheca tubular not bifid; anterior nephridia opening to the outside through a common pore in the dorsal portion of segment III; body cylindrical, not depressed; head not distinct; blunt cylindrical appendages present along the median dorsal line of the body.

Type species: *Pterodrilus alcicornus* Moore, 1895.

KEY TO THE SPECIES OF THE GENUS PTERODRILUS

1. (a) Segments VII and VIII with funnel-shaped enlargements of the dorsal portions; funnel of VIII excavated dorsally so its dorsal margin bears two small "horns".....*Pterodrilus durbini* Ellis, 1919
- (b) Without these funnel-shaped enlargements as described under (a).....2
2. (a) Dorsal appendages on segment VIII only.....*Pterodrilus mexicanus* Ellis, 1919
- (b) Dorsal appendages on more than one segment.....3
3. (a) Dorsal appendages on segments II to VIII, inclusive.....*Pterodrilus distichus* Moore, 1895
- (b) Dorsal appendages on segments III, IV, V, and VIII.....*Pterodrilus alcicornus* Moore, 1895

Pterodrilus alcicornus Moore, 1895

Pterodrilus alcicornus, Moore, 1895a. Proc. Acad. Nat. Sci. Phila. 450-453.

Pterodrilus alcicornus, Pierantoni 1912. Ann. Mus. Zool. Univ. Napoli, N.S. 3(24).

Pterodrilus alcicornus, Hall 1914. Proc. U.S.N.M. 48:190-193.

Pterodrilus alcicornus, Ellis 1919. Proc. U.S.N.M. 55:254.

Description from Moore 1895a:450-453.

"In this species, which is described from sections and specimens mounted entire, the body is terete throughout, or owing to the increase in thickness of the dorsal walls of the major annuli, appears somewhat compressed at these points. The somites VI, VII, and VIII are of about equal diameter, those anterior and posterior to them tapering respectively toward the head and caudal disks. Bi-annulation of the body somites is very marked. The head is rather slender, and consists of a circum-oral annulus divided into thick entire dorsal and ventral lips, and two similar post-oral rings. The caudal sucker is a muscular disk of simple form, and about the diameter of the first post-cephalic somite; its axis coincides with that of the body somites.

"Dorsal organs are highly developed in this species on post-cephalic

somites III, IV, V, and VIII. Somites VI and VII, and in less degree, II also, exhibit slight dorsal thickenings, of the body musculature. On the dorsum of the major annulus of somite III the body walls rise into a high compressed transverse ridge or plate, which fades out on the sides of the somite, and is produced laterally into a conspicuous, forwardly projecting trilobed wing, the anterior division of which flares outward and extends far forward over somite II, usually ending in a slightly bifid expansion. The remaining lobes are simple and conical tines, which project upward and slightly outward. The two wings flare so strongly that the distance between their apices is about $1\frac{1}{2}$ times the diameter of the somite. Their shape is very strongly suggestive of the antlers of a young moose, hence the name given to the species. The generic name was also suggested by this species, in which the dorsal organs have a wing-like aspect not seen in the other species.

"The dorsal appendage of the VIIIth somite is also highly developed, and similar to the one just described. Its lateral wings, however, are less conspicuous, and are directed posteriorly instead of anteriorly, and also flare outward more conspicuously. The whole organ is strongly concave behind, while that on the third somite is similarly concave before. A small gland, closely resembling a clitellar gland, is sometimes present (in two out of three series of sections) embedded in the base of the organ on each side. On the IVth and Vth somites the appendages are less highly developed, but are similar, the low dorsal ridges bearing on each side a pair of slender and simple cylindrical processes.

"The transverse dorsal ridges are built up chiefly of short, thick, longitudinal muscle fibres, which extend between the anterior and the posterior covering of hypodermis. Spaces partly filled with a connective tissue network are observable among the fibres, and a similar more extensive space separates the muscles of the dorsal organ from the longitudinal muscles of the body walls. A few vertical muscle fibres, are also developed in the lateral margins of the ridges. Over this firm muscular basis the hypodermis, with the circular muscle layer, extends, and this alone, with a core of loose, spongy tissue, probably derived from the subdermal connective tissue, forms the terminal processes and lobes. . . . In the formation of these dorsal appendages from the body walls, it would seem that the loose fold of hypodermis and circular muscle fibres that rises freely from the longitudinal muscle fibres is pinched up, as it were, at several points, from which the skin and connective tissue underlying it proliferate to form the marginal processes, while the space remaining becomes filled, save for a few narrow clefts, with muscle fibres that proliferate from the ends of the longitudinal muscle fibres of the body walls at the points where these meet the hypodermis.

"The alimentary canal is enlarged to form a saccular stomach in the

four anterior body somites, while posteriorly it is narrow and tubular, and, with the exception of a slight transverse loop in the VIIth and VIIIth somites, proceeds directly to the anus on the dorsum of somite X.

"The jaws are small, measuring 0.02 mm. in breadth. They are of similar form, being quadridentate, with a median pair of long, sharply-conical, widely-separated, and divergent teeth, bent at a nearly right angle from the plane of the somewhat quadrangular basal plate. In extreme lateral positions are a pair of inconspicuous blunt teeth. When in position the basal plates are fixed in the cuticle of the pharynx, and the points of the teeth of the two jaws cross in the pharyngeal lumen.

"The spermatheca lies in the Vth somite to the left of the intestine. Its lower half is narrow and cylindrical, its upper abruptly expanded.

"The copulatory bursa is rather thin walled, and with the penis is capable of complete invagination. The penis sheath is relatively short, and exhibits no muscular atrial enlargement at the upper end. The glandular atrium is short, nearly spherical, and thick walled. It receives the vasae deferentiae, which are of the usual form. In the mounted specimen from which figure it was drawn, the atrium was twisted so that in the figure the anterior end is directed posteriorly.

"The common opening of the anterior pair of nephridia is located on the dorsum of the major annulus of somite III, immediate posterior to the dorsal appendage.

"The largest examples found among about a dozen specimens measure about 1 mm. in length."

Type: From Johns River, Watauga Co., N. C., on *Cambarus acuminatus*.

Previous locality records:

Moore 1895a:453—

1. Johns River, Watauga Co., N. C., on *Cambarus acuminatus*.

Remarks: This species has not been encountered in the present study.

Pterodrilus distichus Moore, 1895

Pterodrilus distichus, Moore 1895a. Proc. Acad. Nat. Sci. Phila. 453-454.

Pterodrilus distichus, Pierantoni 1912. Ann. Mus. Zool. Univ. Napoli, N.S. 3(24).

Pterodrilus distichus, Hall 1914. Proc. U.S.N.M. 48:190, 193.

Pterodrilus distichus, Ellis 1919. Proc. U.S.N.M. 55:254

Description from Moore 1895a:453-454:

"Dorsal appendages are present on post-cephalic somites II to VIII inclusive, and are much simpler than in *P. alcicornus*. The dorsal ridges are not compressed and plate-like, and are similar on all the somites. On somites II to VII each bears a pair of bluntly pointed cylindrical lateral appendages, while somite VIII bears two pairs, they become somewhat larger anteriorly.

"These appendages contain no longitudinal muscle fibres, and the

ridges on which they rest are largely formed . . . of a muscular network derived from the circular fibres.

"In somites VII and VIII a complete transverse loop is developed on the intestine, which is otherwise as in *P. alcicornus*. The jaws are also very similar, but differ in the shorter median pair of teeth, and the stouter form of the basal plate . . .

"The spermatheca is slender and clavate, and regularly tapers from blind end to mouth. It lies to the left of the intestine. The copulatory bursa is nearly spherical, with thin muscular walls, and larger bursal glands than *P. alcicornus*. Its inner surface is thrown into deep ridges, among which the penis lies. The whole structure when evaginated is shaped not unlike a mushroom, and resembles the corresponding parts of *Bdellodrilus philadelphicus*. The glandular atrium is remarkable in being divided by a deep cleft into two similar lobes, the structure being flattened in a plane perpendicular to this cleft, giving the organ a shape much resembling the conventionalized heart. The penis sheath is short, and lacks a sacular dilation.

"The anterior nephridial pore is on the crest of the ridge of the IIIrd somite. In other respects this species resembles *P. alcicornus*.

"The largest example . . . from among upwards of fifty specimens measured 1.5 mm. in length, the usual size being about 1 mm."

Type: From western New York on *Cambarus bartonii*.

Previous locality records:

Moore 1895a:454—

1. Western New York on *Cambarus bartonii*.

Ellis 1919:254—

1. Oxford, Ohio, host not given.
2. Cedar Point, Ohio, host not given.
3. White River, Irondale, near Anderson, Ind., on *C. rusticus*.
4. White River, Noblesville, Ind., on *C. rusticus*.

New locality records:

1. Oakwood, Ill., on *C. propinquus*.

Remarks: The local material of this species examined agreed closely with Moore's description.

Pterodrilus durbini Ellis, 1919

Pterodrilus durbini, Ellis 1918. Trans. Amer. Micr. Soc. 37:49-51.

Pterodrilus durbini, Ellis 1919. Proc. U.S.N.M. 55:254-255.

Description from Ellis 1919:254-255:

"Body rather short and thick, size small; width of the head scarcely equaling the width of segment I; body segments increasing rapidly in diameter from segment I to segment VII; segment VII (sometimes segment VI) the wide segment of the body; at least 10 body segments visible in side view; major and minor annulations of segment I of about

the same diameter, the major annulation, however, being about twice the length of the minor annulation; major annulations of segments II, III, and IV conspicuously elevated laterally and dorsally, forming ruffle-like bands around the anterior halves of each of these three segments; minor annulation of segment V almost obliterated, major annulation of segment V elevated dorsally and laterally into a midsegmental crest which almost encircles the segment; major annulation of segment VI low, the minor annulation elevated into an encircling segmental crest; major annulation in segment VII elevated and expanded into a funnel-shaped collar which encircles it and stands free from it except at the junction of the segment proper and the collar, the bell of the funnel being directed cephalad; minor annulation of segment VII low; major annulation of segment VIII elevated and expanded into a funnel-shaped collar like that on segment VII, except that the funnel of segment VIII is directed posteriorly, its bell opening caudad and standing free above the low minor annulation of segment VIII; dorsal margin of the funnel-shaped collar of segment VIII excavated in the mid-dorsal line, so that the margin of the funnel shows two distinct "horns" when seen from front or rear; segments IX and X low, small, and regular; head not exceeding the first two body segments in length, divided into three rather equal thirds by two indistinct grooves; lips two, the upper the longer, both slightly emarginate in the median line; oral bristles present; dental formula 5-4; . . . major pharyngeal diverticula two, one dorsal and one ventral; alimentary canal straight, maximum enlargement in segment IV; testes in segments V and VI; vasa deferentia from segments V and VI meeting in segment VI; no accessory sperm tube; spermatheca simple and tubular; caudal sucker large, termino-ventral; its diameter equalling or exceeding the greatest diameter of the head; largest specimen examined 2.0 mm. in length."

Type: U.S.N.M. No. 17655 from White River, Irondale, near Irondale, near Anderson, Ind., on *Cambarus rusticus* Girard.

Previous locality records:

Ellis 1918:50—

1. James Island, Potagannissing Bay, Mich., on *Cambarus virilis* Hagen.
2. Three miles up Potagannissing River, Drummond Island, Potagannissing Bay, Mich., on *C. virilis*.
3. Pilot Harbor, Sitgreaves Bay, north side of Drummond Island, Potagannissing Bay, Mich., on *C. virilis*.
4. Little Cass Island, head of Detour Passage, Mich., on *C. virilis*.
5. Churchville Point, head of Lake George, 46° 31' N, Mich., on *C. virilis*.
6. Winona Slips, Bay City, Saginaw Bay, Mich., on *C. virilis*.

Ellis 1919:254—

1. Anderson, Ind., on *Cambarus rusticus*.

Remarks: The single specimen examined agreed closely with Ellis' description.

Pterodrilus mexicanus Ellis, 1919

Pterodrilus mexicanus, Ellis 1919. Proc. U.S.N.M. 55:254.

Description from Ellis 1919:254:

"The type-specimen was unique, and, unfortunately poorly preserved. Consequently but a brief diagnosis can be given. General body form similar to *Pterodrilus distichus* Moore; no dorsal processes on segments II to VII, inclusive; segment VIII bearing a simple four-horned appendage like that on the same segment of *P. distichus*; dental formula 5-4; As far as the internal anatomy could be traced in a whole mount of this poorly preserved specimen, the organs resembled those of *P. distichus* Moore and *P. durbini*, new species."

Type: U.S.N.M. No. 17654 from Mirador, Vera Cruz, Mexico, on *Cambarus mexicanus* Erichson. Length 1.0 mm.

Previous locality records:

Ellis, 1919:254—

1. Mirador, Vera Cruz, Mexico.

Remarks: This form needs further study but unfortunately no specimens were available to the writer.

GENUS CIRRODRILUS Pierantoni, 1905

Cirrodrilus, Pierantoni 1905. Ann. Mus. Zool. Univ. Napoli, N.S. 1(31).

Ceratodrilus, Hall 1914. Proc. U.S.N.M. 48:190-191.

Ceratodrilus and Cirrodrilus, Stephenson 1930:800-801.

Ceratodrilus, Yamaguchi 1932a. Ann. Zool. Japon. 13:361-367.

Stephanodrilus, (Ceratodrilus), Yamaguchi 1934. Jour. Fac. Sci. Hokkaido Imp. Univ. 3(3):191-215.

With the characteristics of the subfamily; spermatheca simple, not bifid; no accessory sperm tube; anterior nephridia opening to the outside through separate pores in the dorsal half of segment III; penis eversible; body cylindrical, not depressed; with body appendages in the form of pointed bands extending transversely across the dorsal surface.

Type species: *Cirrodrilus cirratus* Pierantoni, 1905, from Japan.

Only known American species: *Cirrodrilus thysanosomus* (Hall, 1914).

Remarks: Hall differentiated *Ceratodrilus* from *Cirrodrilus* on the basis of the dorsal appendages because Pierantoni had described *Cirrodrilus* as having ventral appendages. However Yamaguchi (1932a: 362-365) collected material and found that Pierantoni's specimen was nothing but a poorly preserved worm which he had incorrectly oriented. Yamaguchi (1932a:364-365) summarizes his evidence as follows:

The specimen, on which Pierantoni based his description, was, as he indicated in a poor state of preservation, and could not be used for the investigation of its internal anatomy.

. . . . the main difference between Pierantoni's and my specimens lies in the position of the trunk appendages, while the other characters accord generally with each other.

Before entering upon the discussion of the question the following fact is noticeable. In my specimens, those fixed with Zenker's solution or sublimate-alcohol almost retain the structure of living condition, while those fixed with dilute alcohol are considerably deformed and bear remarkable resemblances to Pierantoni's specimen in pyriform head which lacks the membranous margin and obscures of the lamellar ridge and the annulations of the trunk.

In regard to the difference in number of the head appendages between Pierantoni's specimen and my own, I am of the opinion that his specimen is abnormal or damaged.

The position of the trunk appendages in his specimen, the most distinguishable character of all, seems to me to be doubtful. In his paper no description of the anus, spermathecal pore and male pore is given. Therefore, it must be depended only upon the head in distinguishing the dorsal and ventral surfaces of the worm.

Furthermore, in the figure, the neck is very narrow and the annulations of the anterior part of the trunk obscure. Thus it seems to me possible that in his specimen the head was twisted on account of ill-preservation.

On the basis of the above evidence it seems to the writer that Pierantoni's *Cirrodrilus* and Hall's *Ceratodrilus* are one and the same genus.

Cirrodrilus thysanosomus (Hall, 1914)

Ceratodrilus thysanosomus, Hall 1914. Proc. U.S.N.M. 48:191.

Ceratodrilus thysanosomus, Yamaguchi 1932a. Ann. Zool. Japon. 13:367.

Description:

Head distinct from body; peristomium bilobed, each lobe fringed with four or five papillae; body of relatively uniform diameter throughout although slightly greater in segment VI or VII. Hall (1914:191) gives the following measurements which agree rather well with my material: "Length 2 to 2.6 mm.; maximum head diameter, 400 micra; maximum body diameter 660 micra; maximum sucker diameter, 360 micra. Maximum length of cirriform appendages of head, about 180 micra." Anterior dorsal portion of head with a membranous border deeply incised to form four tentacular appendages; first seven trunk segments have dorsal appendages, extending from the lateral border in a pointed band, the number of points varying from 6 to 8 but usually being 6.

Testes present in segments V and VI with male bursa in VI; without accessory sperm tube; spermatheca in V cylindrical or flask-shaped, simple; penis eversible.

Dorsal and ventral jaws slightly dissimilar with a 7-6 dental formula; teeth of comparatively uniform size. Intestine relatively straight with several sacculations with an anus in the mid-dorsal line of segment X.

Type: U.S.N.M. No. 17708 from streams of the Great Basin, Salt Lake City Utah.

Previous locality records:

Hall 1914:191:

1. Salt Lake City, Utah.

New locality records:

1. Burley, Idaho, on *Astacus gambelii*.
2. Bvours, Ore., (Harney Co., Silver River), on *A. gambelii*.
3. Evanston (Bear River), Wyo., on *A. gambelii*.

NOMINA NUDA

Three species mentioned in the literature have been either incompletely described or remain wholly without description, and since none of these has been recognized under the International Code, these names must be regarded as *nomina nuda*.

Bdellodrilus manus Moore, 1895

Moore (1895a:454): "*Pterodrilus distichus* was found in great numbers with *Bdellodrilus philadelphicus*, *B. manus* n.s." He never described this form or differentiated it in any way.

Branchiobdella chilensis

Moquin-Tandon (1846:300): "Branchiobdelle . . . Gay, lettre à M. de Blainv., Instit., 1936 mars 28.—'Hab. le Chili, aux environs de Santiago, sur les branchies d'une écrevisse (Gay).'"

Branchiobdella auriculae

Moquin-Tandon (1846:301): "Branchiobdelle . . . Gay, lettre à M. de Blainv., Instit., 1936 mars 28.—'Hab. le Chili, trouvée dans la poche pulmonaire de l'Auricula Dombeii (Gay).'"

IX. BIOLOGY

HOST SPECIFICITY

ELLIS (1919) found nearly every form of branchiobdellid that he studied from sufficient number of specimens on a great number of different species of crayfish. Evans (1939) found the species of those worms he studied in Champaign County on all forms of crayfish encountered. The writer's work confirms this, and by adding many new host records for previously described species practically proves that there is no host specificity. For example, *Cambarincola philadelphica* has been found on a great number of crayfish, including *Cambarus bartonii*, *C. obscurus*, *C. dubius*, *C. latimanus*, *C. rusticus*, *C. diogenes*, *C. virilis*, *C. propinquus*, and *C. blandingii acutus*. In short, within the limits of the range of any branchiobdellid any crayfish may serve as host.

FOOD HABITS

Dorner (1865) from observations on European forms believed the food of branchiobdellids was largely the blood of crayfish. Smallwood (1906) thought that *Xironogiton instabilis* and *Bdellodrilus illuminatus* did not feed on the crayfish since their intestine was filled with algae. Hall (1914) believed young animals to be non-parasitic but adults to be parasitic in their food habits. Yamaguchi (1934) thought the gill-inhabiting species fed on the blood of the host, but the others did not.

After examining a large number of specimens containing food in their intestine, the writer has come to the conclusion that in most forms diatoms are the favorite food during all stages of their life. Other things were found, as parts of very small insect larvae, algae, and in many cases immature individuals of the same species. In many instances worms were found with the gut fairly extended with small diatoms. As a result the writer concludes that while some species may occasionally take food from their host, in general most forms are non-parasitic and feed largely on diatoms. If some are parasitic they are probably only facultative parasites.

LONGITUDINAL DISTRIBUTION OF BRANCHIOBDELLIDS IN A STREAM

"Spotty" field collecting at various places gave the impression that the distribution of these worms in a stream was independent of size or drainage area. In order to check this hypothesis, Spanish Needle Creek, a stream about twenty miles long, was selected and crayfish were collected from source to mouth. Collections were also made at several points in Macoupin Creek, to which Spanish Needle Creek is a tributary.

Spanish Needle Creek is located in the central part of Macoupin County, Illinois. This stream has a sand and rock bottom throughout its entire course and has water in it almost to its source even during the driest months of the year. The creek has the typical invertebrate fauna of a central Illinois stream, including large numbers of dytiscid, gyrenid, and hydrophilid beetles; corixid, notonectid, and gerrid bugs, amphipods (*Gammarus*), and isopods (*Asellus*).

The first station for collecting was near the source. Here the water was less than a foot deep and the stream was very narrow with low banks. In this place were found large numbers of the crayfish *Cambarus virilis* and *C. blandingii acutus*, all possessing in great numbers *Cambarincola macrodonta*.

Station 2, about $1\frac{1}{2}$ miles down stream, had a much greater volume of water. The creek here was about $1\frac{1}{2}$ feet deep and steep banks were beginning to form. Here again were found *Cambarus virilis* and *C. blandingii acutus*, all having large numbers of *Cambarincola macrodonta*.

Station 3, about the median portion of the stream, was very rocky, with numerous rapids. The water averaged about 2-3 feet deep with many holes which were much deeper. At this point the stream was very wide, and steep high banks were formed. Nearby a fairly large tributary entered. Although the character of the stream had changed greatly, *Cambarus virilis* was found to harbor *Cambarincola macrodonta* in about the same numbers.

The water at Station 4, near the mouth of the stream, was about 4 feet deep with many deeper holes. It had a smooth sand bottom. Here around the roots of trees that extended into the water, *C. virilis* again was found in great numbers, still harboring *Cambarincola macrodonta*.

Station 5 was at the mouth of the stream where it flowed into Macoupin Creek. Here the water was 5-6 feet deep but the crayfish collected carried the same worms. A few collections were made in Macoupin Creek itself, and the worms were found to be of the same species as was found in Spanish Needle Creek.

This study seemed to confirm the tentative conclusion that the distribution of branchiobdellids in a stream is independent of size and drainage area.

X. CONCLUSIONS

SO FAR AS IS KNOWN, there are nine genera and twenty-one species of Branchiobdellidae in North America. These are:

<i>Branchiobdella tetradonta</i>	<i>Xironodrilus pulcherrimus</i>
<i>Branchiobdella americana</i>	<i>Bdellodrilus illuminatus</i>
<i>Cambarincola elevata</i>	<i>Stephanodrilus obscurus</i>
<i>Cambarincola inversa</i>	<i>Triannulata magna</i>
<i>Cambarincola vitrea</i>	<i>Triannulata montana</i>
<i>Cambarincola macrodonta</i>	<i>Pterodrilus durbini</i>
<i>Cambarincola chirocephala</i>	<i>Pterodrilus mexicanus</i>
<i>Cambarincola philadephica</i>	<i>Pterodrilus distichus</i>
<i>Xironogiton occidentalis</i>	<i>Pterodrilus alcicornus</i>
<i>Xironogiton instabilis</i>	<i>Cirrodrilus thysanosomus</i>
<i>Xironodrilus formosus</i>	

The family is divided into two subfamilies. Branchiobdellinae with one pair of testes and Cambarincolinae with two pairs of testes.

One new genus, *Triannulata*, is recognized and defined.

The generic name *Ceratodrilus* Hall, 1914, is believed to be a synonym of *Cirrodrilus* Pierantoni, 1905.

The genus *Cambarincola* is found to be divisible into two subgenera, *Cambarincola* and *Coronata*.

Cambarincola elevata, *Stephanodrilus obscurus*, *Triannulata magna*, and *Triannulata montana* are described as new species.

Xironogiton oregonensis Ellis is considered to be a western subspecies of *Xironogiton instabilus* (Moore).

Xironodrilus pulcherrimus is found to be divisible into two subspecies due to differences in jaws. These are called *Xironodrilus pulcherrimus pulcherrimus* and *Xironodrilus pulcherrimus dentatus*.

The presence of an accessory sperm tube, the number of anterior nephridial openings, the general shape of the body, the presence and shape of appendages, and gross morphological structures, as clear glands of *Bdellodrilus*, etc., are considered to be of generic importance.

Keys are provided for the identification of all known North American species.

Branchiobdellids have little if any host specificity.

Branchiobdellids apparently are distributed in a stream independent of size of stream or drainage area.

The food of branchiobdellids consists principally of diatoms.

The west coast fauna was found to be closely related to the Oriental fauna. The genera *Cirrodrilus* and *Stephanodrilus* are common to both faunas. *Stephanodrilus* has been first reported from North America in the present work.

A great deal of additional work needs to be done, as whole regions of the United States are unknown so far as this group is concerned and no complete life history has been worked out for these forms.

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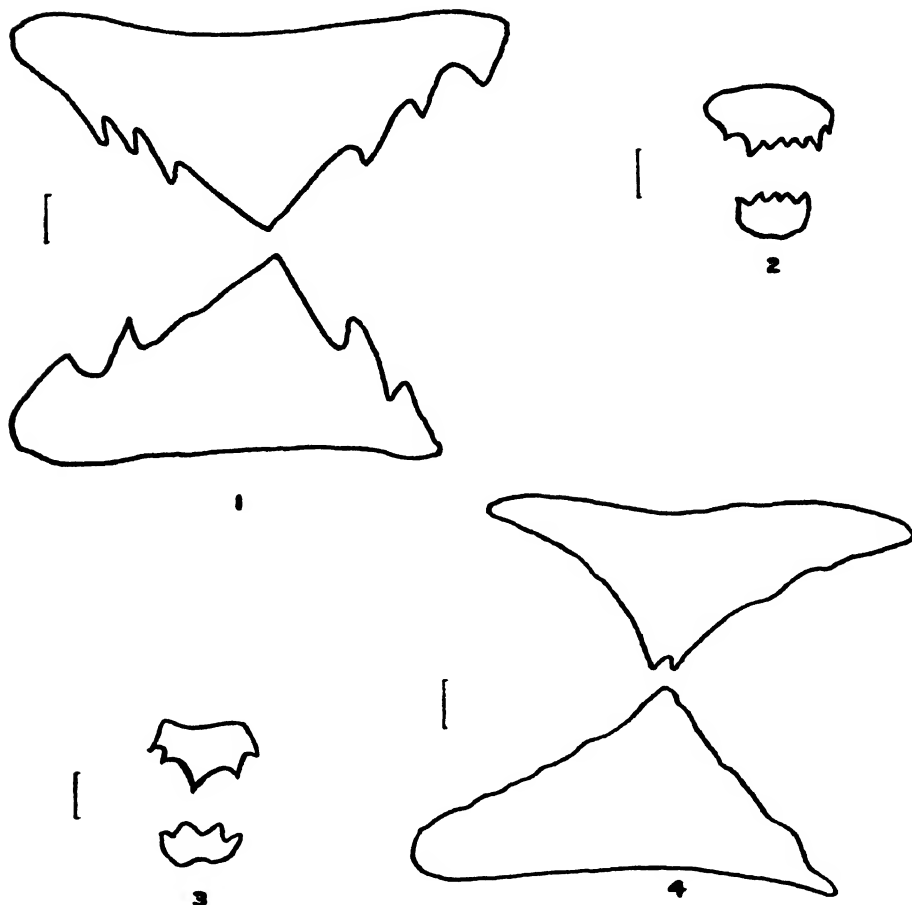


PLATE I

Each line represents 0.02 mm.

(All figures drawn with camera lucida.)

FIG. 1.—Jaws of *Triannulata montana* new species.

FIG. 2.—Jaws of *Stephanodrilus obscurus* new species.

FIG. 3.—Jaws of *Cambarincola elevata* new species.

FIG. 4.—Jaws of *Triannulata magna* new species.

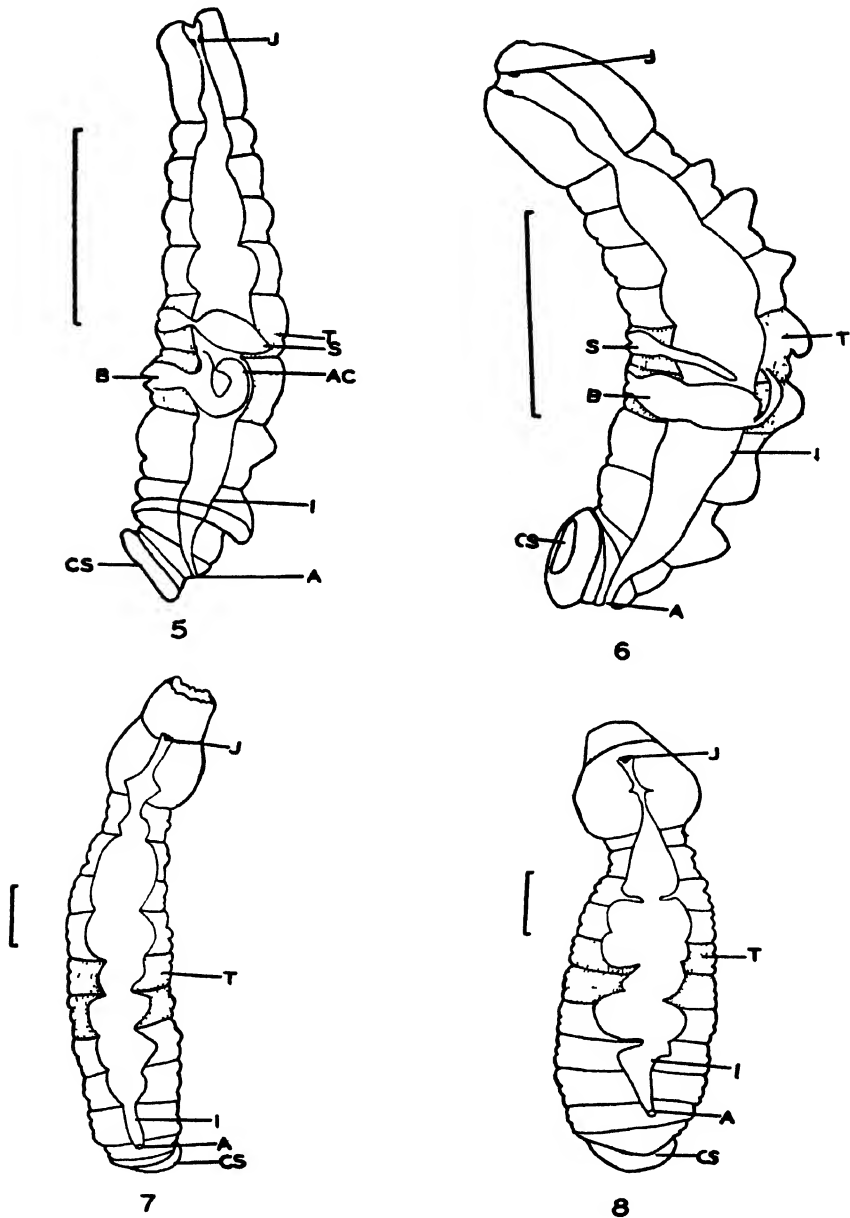


PLATE II

Each line represents 0.5 mm.

(All figures drawn with Eddinger projector)

FIG. 5.—Lateral view of *Cambarincola elevata* new species.FIG. 6.—Lateral view of *Stephanodrilus obscurus* new species.FIG. 7.—Dorsal view of *Triannulata montana* new species.FIG. 8.—Dorsal view of *Triannulata magna* new species.

Abbreviations: A—anus. AC—accessory sperm tube. B—male bursa.

CS—caudal sucker. I—intestine. J—jaw. S—spermatheca. T—testes.

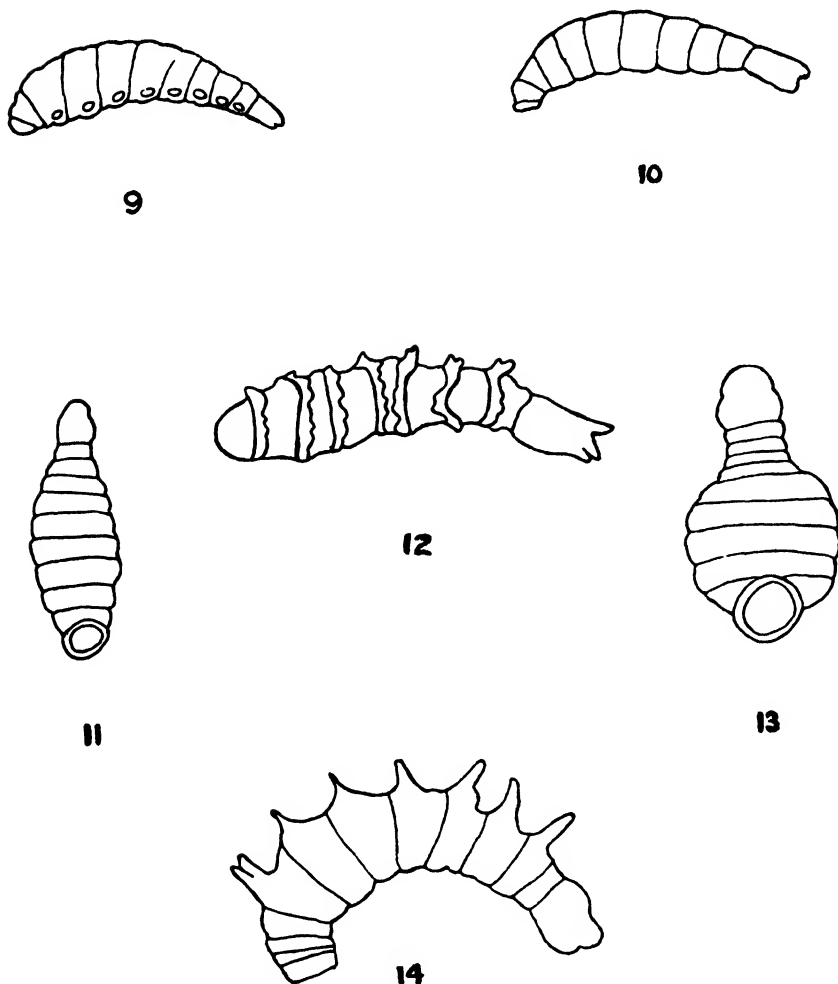


PLATE III

(Figures modified from various sources)

- FIG. 9.—Lateral outline of *Bdellodrilus* Moore.
FIG. 10.—Lateral outline of *Cambaricola* Ellis.
FIG. 11.—Ventral outline of *Xironodrilus* Ellis.
FIG. 12.—Dorsal outline of *Cirrodrilus* Pierantoni.
FIG. 13.—Ventral outline of *Xironogiton* Ellis.
FIG. 14.—Lateral outline of *Pterodrilus* Moore.

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**CYTOLOGICAL OBSERVATIONS ON
ENDAMOEBA BLATTAE**

WITH EIGHT PLATES

**BY
PAUL A. MEGLITSCH**

**CONTRIBUTIONS FROM THE ZOOLOGICAL LABORATORY OF THE
UNIVERSITY OF ILLINOIS
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I. INTRODUCTION

CELL STRUCTURE, and especially nuclear structure, is similar in the majority of metazoan groups. Detailed morphological differences are numerous, of course, even within comparatively restricted systematic limits, but these differences are confined to relatively unimportant minutae, and do not appear to be associated with far-reaching distinctions of taxonomic and phylogenetic importance. The basic morphological pattern of metazoan cells includes a vesicular nucleus with basophilic material suspended in a reticular or structureless matrix of karyolymph. Insofar as the writer is aware, the distribution of basophilic material coincides, or practically coincides, with the distribution of the material which reacts positively to the Feulgen nucleal test in all cases which have been studied. The majority of cytologists consider the basophilic nucleic acid-containing material as chromatin. During division almost all metazoan cells undergo mitotic phenomena which, but for slight variations in detail, follow the same course in all types of organisms. Meiosis, likewise, is similar in all Metazoa in its more general aspects. Thus we may consider the metazoan nucleus a comparatively fixed structural and physiological unit.

Such uniformity does not prevail among the Protozoa. Not only do distantly associated groups have nuclei with fundamentally different structure, as, for example, the vesicular nucleus of the Sarcodina and the massive macronucleus of the Ciliata, but relatively closely related forms, particularly among the Sarcodina, have nuclear patterns with significant differences. Although nuclear phenomena are but incompletely understood it appears that the divergence from the typical metazoan pattern, as observed in some groups, is quite fundamental.

Several factors appear to be important in bringing about nuclear diversity in Protozoa. One of the most important is the tendency toward nuclear specialization. In many of the protozoan groups nuclei are set aside for the consummation of specialized functions. Nearly all ciliates have macronuclei and micronuclei, apparently differentiated primarily for metabolic and reproductive functions respectively. A somewhat similar nuclear specialization is found in the trypanosomes, where a so-called kinetonucleus is distinguished from a trophonucleus, the former appearing to be associated with locomotive phenomena and the initiation of division, while the latter is associated with metabolic functions. Specialization of vegetative and generative nuclei is found among some of the Sporozoa. In the Myxosporidia nuclear specialization is carried still further. The developing pansporoblast contains shell nuclei and capsulogenous nuclei which appear to govern the differentiation of the spore membrane and polar capsule respectively. That so many cases

of nuclear specialization are associated with a segregation of reproductive from metabolic functions suggests that we have to deal with a segregation of reproductive chromatin or idiochromatin from somatic chromatin or trophochromatin. This concept was extremely popular at the turn of the present century and has since been utilized to interpret many nuclear phenomena among the various types of Protozoa. Since this possible separation of a "germ line" from a "somatic line" is not accompanied by histological differentiation as it is in the Metazoa, the nucleus itself must bear the brunt of the specialization.

Instead of specialization of whole nuclei the Amoebae present a long series of slightly differing nuclear patterns which may be extremely simple, as in *Vahlkampfia*, or highly complicated, as in some of the *Endamoebidae*. This high degree of variability may be an expression of the tendency to segregate trophochromatin from idiochromatin. Morris (1936) suggests that this may be the case in *Endamoeba blattae*. Whatever the causes underlying the diversity of nuclear structure in the amoebae, the fact remains that nuclear morphology is an important taxonomic character. Relationships are postulated through the comparison of interphase and kinetophase nuclei. As might be anticipated the diversity of nuclear structure is accompanied by differences in the pattern which appears during division. A series extends from the simple, almost amitotic division of *Vahlkampfia* to highly complicated division types closely resembling metazoan mitosis, as in *Entamoeba histolytica*, and to equally complicated karyokinetic figures, as in *Endamoeba blattae*. So striking are the differences in these division figures that some investigators have hoped to learn something of the development of mitosis through the study of primitive types of amoebae. Most of the phylogenetic speculation dealing with the amoebae has been based primarily on a comparison of interphase and dividing nuclei.

As a result of the variation in the location and appearance of the nuclear elements of the amoebae, the distribution of the basophilic material, commonly known as chromatin, is extremely varied. The identification of chromatic elements in the nucleus is difficult in some cases, for the Feulgen nucleal preparation which is, to some extent, a test for thymonucleic acids, fails to react with the basophilic material found in the nucleus. Thus Morris (1936) and Sassuchin (1936) report that the nucleus of *E. blattae* was not colored by the Feulgen nucleal reaction, indicating that if any thymonucleic acids were present they were either chemically combined in such a way that the color reaction did not occur with the Feulgen reagents as applied, or that normal nucleic acids were present, but in quantities too minute to call forth a visible color reaction. Chalkley (1936) found that in *Amoeba proteus* the peripheral basophilic material was not colored by the Feulgen reaction, but that a cen-

trally placed karyosome reacted positively. The morphological relationship of chromatin—or at least the basophilic constituents of the nucleus—to nucleic acids is not understood in most members of the group.

Critical, detailed studies on the morphology of the interphase and dividing nuclei of different amoebae are essential if generic relationships and the implications of the differing structural patterns are to be understood. Such studies may reveal fundamental correlations between the distribution of basophilic constituents and of thymonucleic acids, and may shed some light on the functional significance they have in the consummation of nuclear activities during the life cycle of the organism.

It is with the problems outlined above that the present investigation deals. The large unusual nucleus of *E. blattae*, while attracting the attention of a number of investigators for the ease with which it can be studied, is still but incompletely known. A number of past investigations have resulted in contradictory results, and much work of confirmation alone is needed. The failure of the Feulgen nuclear reaction to reveal nucleic acid in the nucleus during the interphase is a striking example of the unusual conditions prevailing in this species. Sassuchin (1936) reported that he had failed to obtain a positive response to the Feulgen reaction, but suggested that studies of different stages in division and in the life cycle might reveal the presence of nucleic acid at particular stages.

Since the writer has used the Feulgen nuclear reaction a great deal in the present investigation, an explanation of his use and interpretation of this reaction may be valuable. It is an obvious criticism that this reaction is not a specific microchemical test of known validity for thymonucleic acids, as it can also react with other substances which are present in the cell. For example, plasmogen in the cytoplasm reacts positively. This substance was removed by exposing the slides to 95 per cent alcohol for from 12 to 24 hours. In some cases this substance was still present in small quantities, and the cytoplasm was colored lightly by the reaction. Since it occurs in the cytoplasm, however, it could scarcely be mistaken for nucleic acids occurring in the nucleus. A plasmogen reaction was observed in amoebae in which no reaction could be found in the nucleus, and in other amoebae in which no cytoplasmic reaction had occurred there was a nuclear reaction. Other cytoplasmic substances may react positively, but insofar as the writer is aware, the only substance which might react positively in the nucleus are the nucleic acids. Additional evidence in favor of the view that the reacting substance was nucleic acid was supplied by fixation in absolute alcohol and subsequent washing. According to Fischer (1899) and Mann (1902) nucleic acid is precipitated by alcohol. Slides of *E. blattae*, with control slides of the ciliates *Nyctotherus ovalis* and *Balantidium praenucleatum*, were fixed in absolute

alcohol and were found to react positively to the Feulgen test if there was a minimum exposure to water. The deep coloration of the macronuclear spherules of *Nyctotherus ovalis* was typical in all respects. These spherules are thought to contain nucleic acid (see Kudo, 1936). But nucleic acid precipitated by absolute alcohol is soluble in water, according to Mann and Fischer. Slides fixed in absolute alcohol and washed for 48 hours in running tap water failed to show a positive reaction for ciliates or amoebae in thin sections. Similar smear preparations were negative for the amoebae, and for the ciliates a faint coloration in the center of the macronucleus occasionally occurred in a few organisms lying in the thicker portions of the smear, while the majority failed to show any reaction. Just such a response to the technique used would be expected from nucleic acids. According to Mann and Fischer, nucleoproteins are also precipitated by absolute alcohol, but are insoluble in water after precipitation. This seems to offer some experimental proof in favor of the view that it was nucleic acid which reacted with the Feulgen reagents in the present study, and not nucleoprotein. With these few indications, and willing to admit that the specificity of the Feulgen reaction may be considered as doubtful, the writer considers the material in the nucleus of *E. blattae* which reacts positively to the Feulgen test to be, in all probability, nucleic acid. Until the development of new microchemical tests of greater validity for checking our results we are forced to work with whatever means are at hand. It is with this in mind that the present problem has been undertaken. The writer has interpreted the material reacting positively, then, throughout the present paper, as nucleic acid, not in the more strict chemical sense, but in a loose, cytological sense.

In this study a comparison of results proceeding from the use of basic dyes and the Feulgen reaction were made in order to determine the relationship of basophilic material to nucleic acids, as demonstrated by the Feulgen reaction, throughout the life cycle up to the formation of the mature cyst, following here the suggestion made by Sassuchin (1936) mentioned above, although when the work was undertaken the writer was unfamiliar with Sassuchin's publication. At the same time it was possible to search for new information concerning the morphology and life cycle of the amoeba, and to confirm some of the observations of earlier investigators. As a result of the study, in addition to details of nuclear division during the trophic and cystic stages, it has been possible to observe a cyclical variation in the quantity and distribution of nucleic acid, as determined by the Feulgen test, correlated with the processes of nuclear division and encystment. Several unusual relationships between the basophilic material and the nucleic acid-containing material have also been observed.

II. ACKNOWLEDGMENTS

THE WRITER wishes to express his deep appreciation of the aid given him by Professor R. R. Kudo, at whose suggestion the problem was undertaken. His encouraging and helpful suggestions have unfailingly proved stimulating and without them the work could never have been completed. His thanks are also due Professor W. Shumway and Professor H. J. Van Cleave for suggestions and advice. To various other members of the staff of the Department of Zoology at the University of Illinois the writer wishes to express his regard for their criticisms and suggestions. The writer also wishes to express his thanks to Mrs. Alison Meglitsch for preparing the plates and text figures.

III. MATERIAL

Endamoeba blattae occurs in the anterior dilated portion of the colon of at least three species of cockroaches, *Blatta orientalis*, *Periplaneta americana*, and *P. australasiae*. The oriental cockroach was the source of the amoebae used for this investigation. It is very abundant on the University of Illinois campus and may be collected in large numbers from early spring to late fall. During the day the insects retreat into crevices in the walls of the buildings. At night they emerge to feed and can be captured easily with the aid of a flashlight.

They were kept in battery jars, from fifty to a hundred roaches living well in a single container. A variety of foods were tried, including Fleischman's yeast cakes, moistened soybean meal, potatoes, and apples. As reported by Kudo (1926) the yeast cakes form a most satisfactory diet, not because the insects fail to thrive on the other diets tried, but because the protozoan fauna respond unusually well to the yeast cake diet.

In cockroaches kept in a relatively crowded condition for several weeks in the laboratory the incidence of infection rose to almost 100 per cent. In nature, of course, such high incidence is not usually observed. Kudo (1926) reported that the percentage of infection is lowest in nature in spring and late fall when it falls to about 5 per cent. It is highest during the summer and early fall, reaching a peak of about 50 per cent in July, August, and September. Similar seasonal variation in incidence of infection of cockroaches just captured is recorded by the author. The incidence of infection was maintained at a high level throughout the winter in the animals kept in the laboratory, but for some reason it fell appreciably during early spring every year, although conditions under which the host animals were kept remained constant throughout. This was the more inexplicable since the large ciliate *Nyctotherus ovalis* was as numerous in these hosts as it had been during the

winter, and the smaller ciliate *Balantidium praenucleatum* appeared to be increasing in number at this time.

In immature hosts there is no appreciable difference in the incidence of infection between male and female insects. But a small percentage of adult males harbor amoebae, however, and a heavy infection in such hosts is extremely rare. The mature females, on the other hand, are as heavily infected as the immature insects and approach 100 per cent in incidence of infection. One factor concerned in this difference appears to be the small amount of food consumed by winged males, whose colons are frequently almost empty and greatly shrunken, in contrast to the large amount of food consumed by the voracious females, which have a very large and well filled intestinal tract.

IV. METHODS

LOCKE'S SOLUTION proved to be a very satisfactory medium for maintaining amoebae for periods long enough to complete the necessary procedures. The Locke solution was made with a reduced NaCl content (0.45 per cent) and other compounds reduced proportionately. This was the optimum concentration for survival as revealed by a series of tests for maximum survival time in varying dilutions. When observations were to be made *in vivo* the amoebae were kept in small (20 mm.) petri dishes in sterilized Locke plus 0.5 per cent to 1 per cent Difco albumin. They remained alive and active in this medium for several days if a part of the dissected colon was left in the culture. Many of the amoebae died after from two days to a week. The survivors appeared to adapt themselves to their environment and remained alive and more or less active after a month in many instances. Subculture was not effective, however, as multiplication was quite rare among the cultured amoebae.

Depression slide mounts were used only when a single organism was to be studied for an extensive period of time. Usually the amoebae were kept in petri dishes, removed for observation whenever necessary, and then replaced in the petri dishes. This method allowed greater freedom and proved to be less laborious than the depression slide method. It was especially well adapted to study with vital dyes, where it was not necessary to observe the same specimen continuously in some experiments. Vital dyes were kept in 1-1000 and 1-10000 solutions in Locke, and were diluted with Locke-Albumin to the desired concentration just before use. Of a number of vital dyes tried, Janus green B, Bismarck brown, brilliant cresyl blue and neutral red were the most satisfactory. The optimum strength for these dyes varied between 1-50000 and 1-100000. When a large amount of debris was present in the teased colon a larger amount of dye was needed.

TABLE I
SUMMARY OF NUCLEAR FIXATIVES USED

Simple (Uncombined) Fixatives	Compound Fixatives
<i>Strong</i>	<i>Strong</i>
1. Absolute Alcohol*	1. Gilson Carnoy*
2. Glacial Acetic Acid*	2. Schaudinn*
3. 10% Acetic Acid*	3. Carnoy*
4. 40% Formaldehyde*	4. Gilson*
5. Saturated Aqueous Mercuric Chloride*	5. Sublimate Alcohol*
6. Saturated Aqueous Picric Acid*	6. Sublimate Acetic*
7. 1% Chromic Acid*	
<i>Medium</i>	<i>Medium</i>
8. 5% Acetic Acid*	7. Zenker*
9. 2% Acetic Acid	8. Bouin*
10. 3% Mercuric Chloride	
11. 1% Acetic Acid	
<i>Weak</i>	<i>Weak</i>
12. 4% Formaldehyde	9. Flemming with Acetic
13. 0.5% Acetic Acid	10. Flemming without Acetic
14. 2% Osmic Acid	11. Champy
15. Osmic Vapor	12. Altmann
16. 70% Alcohol	13. Regaud
17. 30% Alcohol	
18. Dioxane	

*Denotes that the fixatives were used at room temperature and at 45-50° C. All others were used only at room temperature.

Permanent mounts for the study of cytoplasmic inclusions were made in toto and in sections 3 to 8 μ thick. Altmann, Regaud, Champy and Flemming without acetic were used as mitochondrial fixatives and were followed by Heidenhain's haematoxylin, Regaud's haematoxylin, Bensley's copper haematoxylin, Altmann's fuchsin-picric acid, Bensley's fuchsin-methyl green, Kull's fuchsin-aurantia-toluidine blue or Benda's alizarin-crystal violet. By far the most satisfactory stained mounts were obtained in material in which the whole colon was fixed with Altmann or Champy and sectioned at 3 to 5 μ , followed by staining in Benda's technique. Golgi material was studied with Kopsch and Kolatchev osmium methods and the da Fano silver technique.

Studies of the nucleus were made with living amoebae under oil immersion in bright and dark field illumination. Permanent mounts were made in toto and in sections cut from 2 to 10 μ in thickness. Except for the finer details of nuclear structure the thick sections proved more practicable.

A number of fixatives were used, chosen for the satisfactory quality of results obtained in preliminary trials. A summary of the fixatives used is given in Table I. The compound fixatives most used were numbers

1, 2, 3, 7, 8, and 9. A number of others not mentioned were tried and gave unsatisfactory results or were not used to any great extent because the results were not significantly different from those obtained with the standard protozoological fixatives.

Fixation and staining so completely alter the appearance and structure of the nucleus of *E. blattae* that it is impossible to describe the fixed and living nucleus in similar terms without very careful study. So many structures can be seen only in fixed nuclei that it was necessary to determine their position in the living nucleus before their interpretation was possible. The correlation between living and fixed nuclei was obtained by a study of the phenomena accompanying fixation. This study included all simple or uncombined fixatives shown in Table I, and numbers 1, 2, 3, 6, 7, 8, and 9 of the compound fixatives.

Amoebae were kept in Locke solution without albumin or were washed before use, for when fixative was added to a solution with albumin in it, the precipitation of the albumin obscured the amoebae. The organism selected was put on a slide in a small drop of Locke solution and a cover glass applied. By using the less viscous mineral oil in place of cedar oil it was possible to carry on observation under oil immersion. A piece of paper toweling was placed in contact with the cover slip at one side of the slide, to draw off the fluid until the amoeba was compressed, but still alive and able to move slightly. This compression was necessary, for amoebae not treated in this way were either carried away with the fixative, or were rendered too opaque for accurate observation. The nucleus was usually slightly compressed also, but insofar as could be determined the structure was not changed, and the parts retained their normal relationships.

The compressed nucleus was studied briefly under oil immersion. When the position of the various regions and structures had been determined, a drop of the fixing solution was placed in contact with the cover glass opposite the paper toweling, which drew it under the cover glass very rapidly. By this method the fixation could be watched under high magnifications and the results determined. Several times dark field illumination was used, but the precipitation of the protoplasm caused so much refraction that it was not continued as a routine practice. Indeed, even in the living nucleus nothing could be seen in dark field that could not also be seen in bright field illumination. When fixation was slow, a very rare condition, the sequence of the appearance of nuclear structures invisible in life was determined. Usually the process reached completion almost instantaneously, or at most in a few seconds, so that it was necessary to repeat many times, fixing the attention successively on

first one and then another region of the nucleus before the complete process could be ascertained. In order to identify the nuclear structures found, their affinity for basic dyes was determined at the end of the experiment by adding acetocarmine or methyl green to the preparation, after appropriate washing. During the whole procedure the nucleus was kept under constant observation.

This study of the process of fixation was very helpful in determining the relationship of the structures in the fixed nucleus to those observed in the living nucleus, and aided in obtaining a reasonably complete understanding of the morphological effects of fixation. By combining the study of the structure immediately following fixation with that of similarly fixed nuclei in stained permanent mounts, some idea of the effects of dehydration were also gained. Each fixative, simple or compound, so studied was used in preparing permanent mounts in toto and in sections, stained with Feulgen's nucleal reaction, Heidenhain's haematoxylin, and Safranin light green, following a rigidly standardized staining procedure.

A. FEULGEN'S NUCLEAR REACTION

After washing for 12 to 24 hours in 95 per cent alcohol the smears and sections were hydrated and passed into the hydrolizing solution where they were held for 5 minutes at 60° C., rinsed in cold hydrolizing solution 1 minute, put into the fuchsin sulphurous solution for one and a half hours, washed in 3 changes of sulphurous acid wash water, 10 minutes each, and in running dechlorinated tap water for 30 minutes. Following dehydration to 95 per cent alcohol the slides were lightly counterstained with light green (10 seconds in a slightly basic 0.5 per cent solution in 95 per cent alcohol) and mounted in balsam after clearing in xylol.

B. HEIDENHAIN'S HAEMATOXYLIN

Slides were mordanted for 5 minutes at 45° C., after which they were rinsed a total of 5 minutes in 3 changes of distilled water. They were stained in 0.5 per cent haematoxylin for 5 minutes at 45° C., washed in running dechlorinated tap water for 20 minutes, and differentiated in large lots in saturated aqueous picric acid. The destaining process could not be standardized perfectly because slight variations in thickness were sufficient to alter the time required to reach maximum contrast. A partial standardization was effected by differentiating large numbers of slides simultaneously, a very effective method for materials sectioned at the same thickness. The differentiation of smear preparations, naturally, could be but incompletely standardized even by this method.

C. SAFRANIN

After postosmication in used Flemming fixative for 15 minutes, and a wash of equal duration the slides were placed in Zwaardemaker's Safranin for one hour and washed in distilled water for 5 minutes. The preparations were then placed in 70 per cent alcohol for 30 seconds, 95 per cent alcohol plus $\frac{1}{2}$ per cent light green S. F. yellowish to deepest contrast (30 seconds to 1 minute according to fixation), rinsed by dipping into 95 per cent alcohol, left in absolute for 30 seconds, and passed into xylol.

Before the warmed haematoxylin method was settled upon for the standardized technique it was compared carefully with the cold method, using both mordant and stain for 12 hours. In all essentials the results were exactly comparable, differing only in the tint of the result. The warmed haematoxylin tended to give deep violet-black nuclear structures, while the cold method produced an even deeper brownish black. Similarly various agents for differentiating haematoxylin were tried. Picric acid gave the sharpest differentiation, and iron alum was next best.

For purposes of comparison a number of other staining techniques were tried. Paralleling the standardized techniques used with the simple fixatives a series of slides stained with Giemsa were made. Occasionally other stains were tried with the simple fixatives, but none were used consistently enough to allow any interpretation of results. Insofar as could be seen with the incomplete data from the other stains, no further structure could have been identified with the other stains tried. With the compound fixatives, however, many combinations were used. These are summarized in Table II.

The large number of stains and fixatives used made it possible to check the results of nearly all the earlier investigators with preparations treated with the same reagents they had used, or with comparable techniques, as determined by a comparison of the effects of different fixatives and stains. This has led to the explanation of some of the discrepancies found in their work.

It became apparent from the study of the material that the nuclear morphology was sometimes altered strikingly by the fixative and stain used. The important differences observed in nuclear appearance after different commonly used fixatives had been employed led to the study of the effects of the simple fixatives, in the hope that some explanation for these discrepancies might be gained. In many cases the action of compound fixatives could be explained from the study of the reagents composing them. The simple fixatives tried are summarized in Table I.

Each simple fixative was studied in the same way. The immediate effects of fixation were determined by observation of the process of fix-

TABLE II
SUMMARY OF STAIN-FIXATIVE TECHNIQUES USED

<i>Nuclear Studies</i>	
Stain	Fixatives*
1. Delafield's haematoxylin.....	1, 2, 3, 4, 5, 6, 8, 9.
2. Ehrlich's haematoxylin.....	1, 2, 3, 4.
3. Heidenhain's haematoxylin.....	1, 2, 3, 4, 5, 6, 7, 8, 9, 10, 11.
4. Borax Carmine.....	1, 2, 3, 4.
5. Paracarmine.....	1, 2, 3, 4.
6. Giemsa.....	1, 2, 3, 4, 5, 6, 7, 8, 9.
7. Safranin.....	3, 5, 6, 8, 9, 11.
8. Safranin-light green.....	3, 5, 6, 7, 8, 9, 10, 11.
9. Safranin-orange G.....	9, 11.
10. Flemming's Triple.....	3, 6, 8, 9, 11.
11. Feulgen's nucleal reaction.....	1, 2, 3, 4, 5, 6, 7, 8, 9, 10, 11.
<i>Cytoplasmic Studies</i>	
12. Heidenhain's haematoxylin.....	10, 11, 12, 13.
13. Regaud's haematoxylin.....	11, 12, 13.
14. Bensley's copper haematoxylin.....	11.
15. Altmann's Fuchsin-Picric Acid.....	10, 11, 12, 13.
16. Bensley's Fuchsin-Methyl Green.....	10, 11, 12, 13.
17. Kull's Fuchsin-Aurantia-Toluidin Blue..	10, 11, 12, 13.
18. Benda's Alizarin-Crystal Violet.....	10, 11, 12, 13.

*The numbers refer to the numbers found in Table I in the Compound Fixative column.

ation under oil immersion, using the technique described above for compound fixatives. Smear preparations fixed with the simple fixatives were made and stained with the three standardized procedures outlined above. Sections 10 μ thick were also stained with these procedures. These permanent mounts were divided into two lots. The first lot was made with a view toward exposing the preparations to a minimum contact with water, at least before the staining process was inaugurated. The second lot was washed for prolonged periods of time in running dechlorinated tap water before staining. Smears were all washed for 24 hours. At first an attempt was made to wash sections for 24 hours also, but later the whole colons were washed for two days before sectioning, and the sections were washed for an additional 12 hours just before they were stained.

As had been expected from the available knowledge concerning the effects of fixation on certain of the more common chemical substances occurring in the nucleus, some of the structures precipitated by simple fixatives were soluble in water, while others were not. By comparing the results obtained from the study of washed and unwashed preparations with the tables of soluble and insoluble substances precipitated by the various fixatives in Mann (1902) and Fischer (1899), it was possible to come to some preliminary and tentative conclusions concerning the com-

position of certain of the nuclear elements. These results were also used to explain the effects of some of the compound fixatives.

V. GENERAL MORPHOLOGY

Endamoeba blattae is one of the largest species of endozoic amoebae known. It attains a maximum size of over $200\ \mu$ and a minimum size of about $45\ \mu$ in the trophic stage. Size distribution varies markedly between these extremes and is affected significantly by the diet of the host. Starvation of the host reduces the number and size of the amoebae. An apple diet also causes a reduction of size, although to a lesser degree. In either case there is a distinct reduction in the number of food inclusions, resulting in beautifully transparent forms. Under such conditions the mean size distribution may shift from 10 to $15\ \mu$ or more. When precystic and cystic amoebae are not present the number of smaller trophic forms is usually distinctly reduced. The highest size frequency usually occurs between 80 and $100\ \mu$ in well fed hosts.

Before the work of Lucas (1927) all amoebae in the cockroach colon were considered as belonging to a single species, *E. blattae*. Thus the size range of this species had always been extended to include the much smaller forms, *Endamoeba thomsoni* and *Endolimax blattae*. Grassi (1882), for example, mentions a number of small amoebae 4.4 to $6.6\ \mu$ in diameter. From his brief description of these tiny organisms it is apparent that he must have observed *Endolimax blattae*. Other early investigators record similar minute dimensions. Some of these investigators believed that the tiny amoebae were recently excysted *Endamoeba blattae*, a view which may have had some basis in fact according to the results of Morris (1936), who describes extremely small, transparent amoebae which emerge from the cyst. Morris was the first to record the size range of the trophic amoebae which has been observed in this study, setting the lower limit of size for the trophic forms at about $50\ \mu$. Precystic amoebae are much smaller than trophic forms, ranging from about 20 to $50\ \mu$, with the largest number between 30 and $40\ \mu$ in diameter. The cysts measure from 15 to $35\ \mu$ in diameter, with the mean around $25\ \mu$.

Cytoplasmic differentiation is apparently of two kinds. A clear, hyaline ectoplasm contrasts with a more granular vacuole-filled endoplasm. A plasmasol-plasmagel differentiation may also be observed. In addition to these, Schubotz (1905) described a so-called "light" and "dark" plasma differentiation. From his descriptions and figures it appears that the dark plasma was the plasmagel and the light plasma the plasmasol, for the distribution of the two types of plasma appears to be identical, as Morris (1936) was led to conclude. Bütschli (1878) and Schubotz (1905) were

unable to distinguish a distinct ectoplasmic layer. Most of the other investigators have observed an ectoplasmic differentiation, however, and Kudo (1926) discusses this point thoroughly. As he points out, a distinct ectoplasmic sheet is but rarely visible and occurs only in comparatively sluggish or inactive amoebae. Small regions of ectoplasm may occur in the anterior or anterolateral margins of active amoebae, but a distinct ectoplasmic layer is not found.

Under high magnifications the plasmasol-plasmagel differentiation is distinctly visible. The plasmagel appears as a more or less continuous reticulum throughout the amoeba in active forms. It is somewhat lighter in color than the plasmasol in life, and stains more intensely with acid dyes, as can be seen in sectioned preparations (Fig. 65). Within the interstices of the plasmagel reticulum lies the plasmasol, a rather granular substance in life, which stains less intensely with acid dyes. Not infrequently a posterior region containing much plasmagel and very little plasmasol can be distinguished in actively motile forms.

During active forward movement striae frequently appear in the cytoplasm. They appear only in active amoebae, and run parallel to the direction of flow of the cytoplasmic currents. These have been described by almost every investigator, most of whom have offered some explanation for their occurrence. Bütschli (1878) and Schubotz (1905) believed that the striae are fibrils formed by longitudinally oriented alveolar walls. Kudo (1926) postulated a stretching of the alveoli in the direction of flow caused by the active endoplasmic streaming which resulted in the striated appearance. Morris (1936) suggested that the plasmasol and plasmagel are immiscible and that the striae are produced by streamers of plasmagel extending into the plasmasol. No observations have been made which will support any of these contentions directly. Concerning the last mentioned possibility, however, it may be noted that streamers of plasmagel do sometimes reach far forward from the posterior gelated region of the amoeba. These have been observed many times in actively moving amoebae, even when striae, which can be seen under quite low magnifications, unlike the plasmagel streamers, could not be found. In other cases striae have been observed with the streamers of plasmagel extending forward between them. The writer is, therefore, of the opinion that the very conspicuous striae are distinct from the delicate streamers of plasmagel. Bütschli (1878) noted that the striae tend to disappear when the amoeba is slightly compressed, which has been amply confirmed during the present study. This observation seems to be inexplicable on the basis of any theory advanced so far, and until further information is available the problem of the nature and mode of formation of the striae must be considered as unsolved.

Locomotion and endoplasmic streaming are very striking in *E. blattae*,

and have been the subject of considerable study. As early as 1898 Rhumbler studied some of the phenomena associated with pseudopodial formation in *E. blattae*. He described cytoplasmic currents accompanying locomotion as "fountain-streaming," characterized by a strong backward flow of plasmasol beneath the relatively thin outer shell of plasmagel. Pseudopodial formation, he noted, is often almost explosive, the current being very rapid and strong.

The speed of forward progression may be quite rapid. Kudo (1926) noted an amoeba which traversed twice its body length in one minute, and several which travelled distances well over one body length per minute. Similar speeds were observed during the course of this study. It appears that active amoebae usually average about one body length per minute, unless very large or hampered by much debris. During active movement the shape assumed is similar to that of *Vahlkampffia limax*. There is a single broad pseudopod, the advancing edge of which may be tipped by a narrow band of ectoplasm or have small anterolateral margins of ectoplasm. Occasionally two pseudopods are formed. Among active amoebae this indicates a sudden change in the direction of movement. Large numbers of lobose pseudopodia, as are formed by *Amoeba proteus*, have not been observed.

In actively moving individuals endoplasmic streaming involves, as explained by Rhumbler, axial and superficial cytoplasmic currents. The axial current advances, moving from the posterior region of plasmagel toward the anterior margin of the pseudopod. There it breaks, fountain-like, to form superficial currents which run posteriorly just under the thin outer layer of plasmagel. A very little of the protoplasm streaming backwards may sometimes return directly into the axial stream, forming an eddy. These eddies, which are comparatively rare, are very striking in amoebae stained with neutral red. The great majority of the plasmasol flowing toward the posterior end of the body is converted into plasmagel at the middle of the body or somewhat anterior to it. Morris (1936, p. 231) says, "Although forward movement of the animal masks the fact during locomotion, it can clearly be seen, when the amoeba is attached by the uroid, that the material which streams forward through the center turns at the anterior end and streams backward along the periphery. There is apparently no anterolateral gelation, nor corresponding reliquefaction in *E. blattae*." The writer cannot confirm this point for amoebae moving actively in a relatively clear field, although the opinion was maintained during the early part of the work. During the observations made on vitally stained amoebae it was possible to trace the course of single granules in the endoplasm during their circuit through the cytoplasm. Granules always showed approximately the

same course. They flowed forward from the posterior end until they reached the anterior tip, where they turned and started to flow backward. The backward flow continued from one-third to one-half of the length of the amoeba during very active movement, and somewhat less during slower movement. At this time the granules ceased to move backward. Using slides with scratches on the surface it was possible to demonstrate that the granules did not change in relation to the substratum from this time until they began to flow forward again, which seems to indicate that a lateral gelation had taken place. It appeared to the writer that at the point at which the supposed gelation occurred there was a reduced amount of Brownian movement. The only exceptions to this were the few granules which became caught in the cytoplasmic eddies which occasionally are found at the anterior end. These enter almost immediately into the anteriorly directed current without continuing backward to the region of gelation. After this had been observed it was sought for in amoebae which were not vitally stained, lest the gelation was an effect of the staining process. With some difficulty the observations were tentatively confirmed in unstained amoebae, although the difficulties in observing unstained small granules made it impossible to be entirely certain of the results.

Not all amoebae show currents which are exactly like those just described. If an amoeba is caught in a mass of detritus, or if it is attached to the slide at one end by the "uroid," streaming without gelation occurs. This confirms the description given by Morris (1936), cited above. It is not a normal locomotory current, however, in that it does not lead to forward progression. When organisms undergo this peculiar type of streaming it sometimes occurs that the superficial backward current flows along only one side of the organism. This results in displacing the usually central axial stream toward the opposite side, and gives the amoeba a peculiar spiral appearance. As when attached by the uroid, this type of streaming apparently does not lead to forward progression. It appears to be identical with the so-called "spiral streaming" described by Sassuchin (1930). It has been observed that during "spiral streaming" gelation in the lateroposterior region of the amoeba occasionally occurs, although it is usually repressed.

Rhumbler's explosive pseudopodial formation in relatively inactive amoebae has been observed frequently. It involves a rapidly moving current of endoplasm breaking through the comparatively rigid ectoplasmic sheet. It is interesting to compare this phenomenon with the formation of pseudopodia in *Amoeba proteus* as described by Mast (1926). He describes a hyaline cap, which is formed as the endoplasm breaks through to the ectoplasmic layer. This seems to be directly analogous to the mode

of formation of the "explosive pseudopodia" in *E. blattae*. It is even more striking in the latter, however, because of the stronger endoplasmic currents and the heavier layer of ectoplasm.

Inactive amoebae are frequently rounded, and bear a large number of small papilliform ectoplasmic protuberances which appear to be formed by the explosive process. In these cases the plasmasol which burst through the gelated region has become gelated and shows no further streaming. Not infrequently one or more of these may be drawn out into a very long pseudopodium containing only hyaline ectoplasm. These are formed very slowly and appear to have no association with locomotion, for the organisms lie quiescent during the whole process. Actively moving amoebae never possess these long hyaline pseudopodia, which persist for but a short time after the organisms bearing one or more of them begin to undergo progressive locomotion. These long pseudopodia appear to be identical in structure with the small ones. Kudo (1926) gives a very accurate description of the small pseudopodia.

VI. CYTOPLASMIC INCLUSIONS

THE PROTOZOAN cytologist has much difficulty in understanding and interpreting cytoplasmic inclusions. So much cytoplasmic differentiation has occurred that many structures not homologous to any found in metazoan cells occur. Some of these structures show affinity for osmium and silver, which is the most important test for Golgi material in metazoan cells. In some cases, as the silver line system of ciliates, no difficulty is met with in distinguishing cytoplasmic inclusions from the unusual specializations of the protozoans. In other cases, particularly in some of the kinetic elements of the flagellates, there has been no unanimity in interpretation, and many discrepancies appear in the literature. Where the cytoplasmic inclusions resemble those found in the metazoan cells which have been studied, interpretation is not so difficult. The osmiophilic material in the cytoplasm of the Sporozoa does resemble osmiophilic material found in invertebrate cells, and it is not difficult to suppose that the two are homologous. But the osmiophilic material around the contractile vacuole of some ciliates is quite different in all respects. Nevertheless it is interpreted by some investigators as being homologous with metazoan Golgi. An added complication has developed from the study of the neutral red vacuome, declared by some cytologists to be the Golgi material and by others to be distinct from it. As a result of these various difficulties there is much confusion prevailing among protozoologists with respect to the Golgi material.

In two groups of Protozoa, the Sporozoa and Sarcodina, the identification of Golgi material seems to be less troublesome than in the other

groups. The morphological similarity of the osmiophilic and the argento-philic inclusions to those found in the metazoan cells aid a great deal in interpreting results. A further aid is found in the fact that there is almost a complete absence of other structures which resemble the Golgi material only in their ability to reduce osmium or silver.

In spite of, or perhaps because of, the relative ease with which Golgi material can be studied in these two groups, it has been rather neglected. A considerable amount of work has been completed on the Sporozoa, but studies on Sarcodina are very few. Causey (1925) studied *Entamoeba gingivalis*. Brown (1930) studied *Amoeba proteus*. Hirschler (1927) made observations on *Endamoeba blattae*. A few added observations have been made by Mast and Doyle (1935), on *Amoeba proteus*. Otherwise the amoebae are wholly unknown. In view of our incomplete knowledge of the Golgi material in the amoebae, *E. blattae* has been restudied, using osmium and silver techniques, with an attempt to correlate the results with those obtained with neutral red and other vital dyes. Some observations were also made on the mitochondria.

A. MITOCHONDRIA

In amoebae stained vitally with Janus green B the mitochondria are stained a light green. They appear as slender rods, usually rather short, which flow about freely in the cytoplasm during the streaming which accompanies movement. The mitochondria appear to be rather adhesive. They are often found adhering to other cytoplasmic granules, and in amoebae stained with Janus green B and neutral red the granules stained red often adhered to the mitochondria. In view of these observations the fact that the mitochondria are occasionally found adhering to the wall of the food vacuoles does not appear to be significant. In many cases there were no mitochondria found on small vacuoles, and many of the mitochondria were not associated with vacuoles. It appears to be safe to conclude that no direct relationship between mitochondria and food vacuoles has been observed for *E. blattae*.

After fixation the mitochondria are shorter and heavier. They usually lie in a small clear area in the cytoplasm. This may be a shrinkage phenomenon. Although no dividing mitochondria were found in vitally stained material, in permanent slides evidences of division have been found. Dumbbell-shaped mitochondria have been found; in several instances two small mitochondria were found in a single clear area. This seems to indicate that the mitochondria divide. No relationship whatever could be found between the occurrence of division in the mitochondria and the stage of nuclear division. During the early part of the precystic period the mitochondria appear to be as numerous as, and morphologically

identical with, the inclusions found in the trophic amoebae. Later precystic and cystic stages have not been observed. Early observations seem to indicate a diminution in number and size of mitochondria in the mature cysts.

B. OSMIOPHILIC AND ARGENTOPHILIC INCLUSIONS

Studies on the osmiophilic inclusions of *E. blattae* were first made by Hirschler (1927). He found two types of osmiophilic inclusions. The larger inclusions were composed of two types of material. An outer osmiophilic region, circular or crescentic in optical section, was contrasted with a more or less spherical inner region of osmiophobic material in the larger type of inclusion. These inclusions measured about $3\ \mu$ in diameter. In addition to the larger inclusions there were a number of smaller inclusions which were quite variable in shape and were restricted to the plasmasol or the dark plasma of Schubotz.

Granules and larger inclusions, apparently identical with those described by Hirschler, were found. His descriptions and figures leave no doubt that the inclusions found were the same as those he had observed. According to Hirschler the smaller granules were lighter than the osmiophilic shell of the larger inclusions. In the material prepared for this study the two osmiophilic components—the smaller inclusions and the osmiophilic shell of the larger inclusions—were approximately equally dark. The difference noted here may be explained by the fact that Hirschler appears to have differentiated further than was the practice in this study.

Argentophilic material appears to be identical in all respects with the osmiophilic material. No difference in appearance or distribution could be found.

A comparison of the osmiophilic material found in *E. gingivalis* as described by Causey (1925) with those found in *E. blattae* shows rather distinctive differences. Causey found a large reticulum which apparently originated from smaller crescentic bodies. These smaller crescentic bodies seem to be similar to the larger inclusions found in *E. blattae*. Small granules which Causey found associated with the food vacuole led him to conclude that these small granules are the primordia of the Golgi material, which is formed from them. Causey's work has been questioned by several investigators, however, who feel that his methods and techniques were not standardized. Thus Nigrelli and Hall (1930, p. 21) say: "The technique used by Causey was not one of the methods used commonly for demonstration of Golgi material and Bowen (1928) has pointed out that Causey's method ordinarily would not be expected to demonstrate elements of the Golgi apparatus. Thence, the occurrence of a

filamentous or net-like 'Golgi apparatus' in *Entamoeba gingivalis* cannot be accepted definitely until Causey's observations have been checked by some of the more commonly used methods for demonstration of Golgi material." Nigrelli and Hall have studied Arcella, and found in that member of the Sarcodina a group of bodies not unlike the larger structures found in *E. blattae*. Brown (1930) found a number of osmiophilic and argentophilic granules accompanied by a smaller number of larger bodies composed of an osmiophilic cortex and an osmiophobic core in *Amoeba proteus*. The larger bodies described by Brown appear to be morphologically similar to those found in *E. blattae*, and the smaller granules also seem similar to the smaller inclusions found in this species.

Exclusive of the work of Causey, then, Golgi material, or, at least, osmiophilic material appears to be generally distributed in two forms. Smaller granules of osmiophilic substances are dispersed in the cytoplasm in large numbers, and larger structures consisting of osmiophilic and osmiophobic parts occur in smaller numbers. The smaller granules may be lacking in Arcella, as Nigrelli and Hall do not mention them. The exceptional case of *E. gingivalis* requires further study before any interpretation can be made. It is interesting to note that the osmiophilic material in the Sporozoa which have been studied is likewise composed of two types of inclusions similar to those found in the Sarcodina (see Hirschler, 1927 and Bowen, 1928).

C. NEUTRAL RED-STAINABLE INCLUSIONS

The use of neutral red as a vital dye for the demonstration of Golgi material has met with some opposition. Neutral red was originally thought to demonstrate the vacuome, supposedly distinct from the Golgi material. The fact that the vacuome, which stains with neutral red, is able to bring about a reduction of osmium has led to the formulation of the opinion that Golgi and the vacuome are either closely related or identical. Hall and his students have found that the neutral red-staining inclusions are identical with the osmiophilic material in a number of protozoan species, including Arcella.

In the case of *E. blattae* no report has been found in the literature concerning the results of intra-vitum staining with neutral red. In dilutions of 1-50000 to 1-100000 it was found that a number of small granules were specifically stained. These small granules were floating freely in the endoplasm. In addition to the granules a number of larger spherical bodies measuring from 3 to 3.5 μ in diameter were stained, although less intensely than the smaller granules. The granules usually acquire a red-violet color in fifteen to twenty minutes exposure, while

after this period the spherical bodies are an orange red. This intensity of color may represent a greater dilution of the stain in the larger bodies, or may possibly indicate a different pH in the two types of inclusions. Almost every one of the larger spherical inclusions have from one to five or six of the smaller granules attached to the periphery. A spherule without at least one granule has never been found. The difference in staining intensity makes it very easy to determine whether or not there are granules adhering to the surface of the spherical bodies.

The spherical bodies are not stained permanently by the neutral red. Their color reaches its greatest intensity in from 15 to 30 minutes after the dye is first applied to the amoeba, when they are a deep orange red shade. This typical coloration persists for several hours, and then gradually becomes less intense. In from 6 to 24 hours colorless spherical inclusions may be found with several intensely stained granules adhering to them. It is possible that this is due to the oxidation of the stain to a colorless leucobase. The smaller granules retain their deep red-violet coloration until after the death of the amoeba.

In the precystic amoebae the conditions are quite different from those just described. The smaller granular inclusions are present in great numbers, distributed at random throughout the cytoplasm. The larger spherical inclusions, however, are not to be found, at least after the nuclear transformation which accompanies the precystic development is completed. During the study of the vitally stained amoebae it was believed that some connection might exist between the larger spherical inclusions and the food vacuoles. This was especially noticeable in several well-fed amoebae from potato-fed hosts. In these specimens a large number of the spherical inclusions were found adhering to the walls of the food vacuoles containing grains of potato starch. The complete relationship of vacuole and inclusion is not as yet understood. It is interesting in this connection to observe that during the precystic period nearly all and finally all of the food vacuoles disappear at the same time that the spherical inclusions disappear. This appears to strengthen somewhat the inference that there is some relationship between the vacuoles and the inclusions.

Granules and spherules, apparently identical with those described above, were also stained with brilliant cresyl blue and Bismarck brown. These two dyes were so much less specific than neutral red, and the amoebae die so much more rapidly that few observations were made with them. No decolorization of the spherical inclusions was observed in amoebae stained with these dyes, but whether this depended on the greater toxicity of the stains or a difference in the chemical nature of the dye could not be determined. A number of other stains were tried.

Unfortunately they were either ineffective or stained so many structures that it could not be determined whether they stained the neutral red-stainable inclusions.

D. INFERENCES

The similarity in size, appearance, and general distribution of the inclusions staining with neutral red and those which were impregnated with osmium and silver appears to be in accord with the observations of Hall and his students on various species of Protozoa. Insofar as this writer is aware, this information was previously available for but one member of the Sarcodina, namely *Arcella*. A number of times confirmation was obtained by impregnation of vitally stained amoebae with osmium. In all cases the stained inclusions were darkened with reduced osmium. Insofar as could be determined such preparations did not differ from the usual Golgi slides in general appearance and distribution of the impregnated inclusions.

The fact that there were two distinct types of inclusions, both of which were stained by neutral red and impregnated with osmium and silver, made it extremely difficult to interpret the results. It has been felt that until some additional information is available regarding the osmiophilic inclusions it would be impossible to determine accurately which type of inclusion is to be considered as a homologue of the metazoan Golgi material. Certainly not all osmiophilic inclusions are Golgi material, and supplementary work must be carried out before any conclusions can be reached.

It is extremely interesting, however, to observe a similarity between the larger type of osmiophilic inclusion and the secretory granules found in some metazoan gland cells. Sharp, in his *Introduction to Cytology* (1934), shows figures of secretory granules from various sources (Fig. 37, p. 76) which appear to be identical insofar as structure is concerned with the larger inclusions occurring in *E. blattae*, *Amoeba proteus*, and *Arcella*. Some of the Sporozoa, also, have osmiophilic inclusions which are similar to the secretory granules. The question as to whether this is merely a coincidental resemblance, or is significant, cannot be settled on the basis of the present data. If, as it appears possible, some relationship between the food vacuole and osmiophilic inclusion can be found, it would seem that there would be an even greater resemblance of the secretory granule to the larger osmiophilic inclusion.

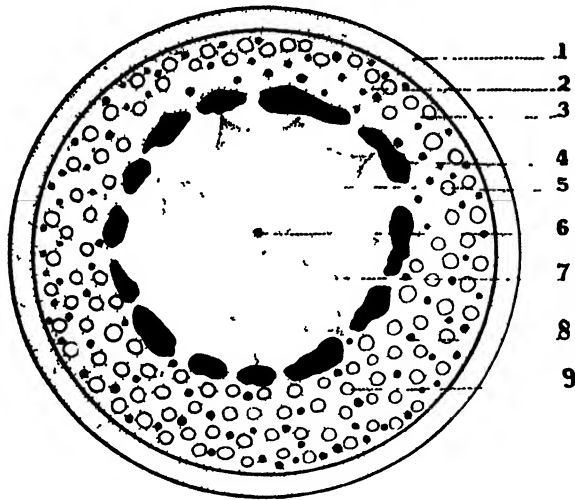
The smaller type of osmiophilic inclusion of *E. blattae* appears to cling to the outside of the larger spherical bodies in amoebae stained with neutral red. The writer believes it possible, at least, that the osmiophilic crescent of the larger spherules may be no more than the accumulation and imperfect preservation of the small granules upon the larger inclu-

sion. This, again, appears to afford another resemblance of the larger inclusion to secretory granules, for it has been supposed that the osmiophilic portion of the secretory granules represents a portion of the Golgi network which remained in contact with the secretory granule after it had been formed. If this relationship of osmiophilic granule to the larger spherical inclusion should prove, on further work, to be correct, it appears that the small granules would be the true Golgi homologue. It is, of course, impossible to conclude, on the basis of the evidence at hand, that the larger inclusions are secretory granules or Golgi material, or that the smaller inclusions are the Golgi homologue, and we await further investigations of the functional relationships of the granules to the spherical inclusions and of the spherical inclusions to the food vacuoles which may possibly throw some light on the question.

VII. TERMINOLOGY USED FOR NUCLEAR DESCRIPTION

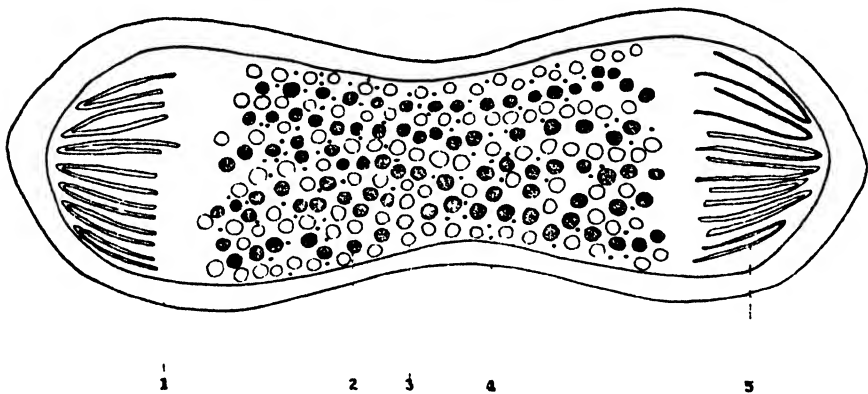
IN ORDER to facilitate interpretation of the descriptive text a diagrammatic representation of the trophic interphase and kinetophase nuclei are given in Text Figs. I and II, with the structures fully labelled. The terms selected, because of the structural differences between the nucleus of *E. blattae* and that of other parasitic amoebae, are in some cases inapplicable if strict homology of similarly designated structures is expected. To preserve the customary terminology as much as possible some concepts have been rather strained. Indeed, in many of the nuclear structures of the Sarcodina great confusion prevails insofar as homology is concerned, and few investigators have attempted to erect a consistent terminology. In the case of *E. blattae*, the previous investigators have frequently referred to the same structures with very diverse terms. Whenever feasible the terms employed by the majority of previous workers are used. Definitions and remarks concerning the terms selected are given below to facilitate comparisons with the descriptions of previous investigators.

Central ground-plasm.—This substance fills the inner part of the intranuclear space. Although not technically a ground-plasm, since the chromosomes are formed from it, its clear, transparent optical character in life and its homogeneous or delicately reticulated, undifferentiated appearance in the fixed condition during interphase give the term some descriptive value. It forms the homogeneous, granular or reticular region which lies within the endosomal girdle in fixed material. It is optically differentiated from the peripheral ground-plasm, with which it is connected at a few points by radii-like extensions in fixed material, or is in contact along the whole margin in material fixed with weak fixatives or in life (Text Fig. I).



TEXT FIG. I. SCHEMATIZED DIAGRAM OF NUCLEUS OF TROPHIC *E. blattae*

(1) Nuclear membrane; (2) peripheral zone; (3) peripheral ground-plasm; (4) endosome; (5) central region; (6) centriole; (7) central ground-plasm; (8) peripheral granule; (9) peripheral spherule.



TEXT FIG. II. SCHEMATIZED DRAWING OF DIVIDING NUCLEUS OF TROPHIC *E. blattae*

(1) Nuclear membrane; (2) endosomal spherule; (3) peripheral spherule; (4) peripheral granule; (5) chromosome.

Central region.—The region lying within the endosomal girdle in the interphase nucleus. This is identical with the central zone of *Sassuchin* (1936) (Text Fig. I).

Centriole.—The small basophilic granules which may sometimes be seen at the center of the central ground-plasm in the interphase nucleus and at the poles in the kinetophase nucleus. Although it could not be

traced accurately throughout karyokinesis, its position and appearance invariably resembled that of a centriole. This is identical with the central granule of Kudo (1926) and the karyosome of Morris (1936) (Text Figs. I and II).

Chromosome.—The strands which appear at the poles of dividing nuclei, and whose anlage may be seen in the central region during early division stages. They contain free thymo-nucleic acid as determined by the Feulgen nucleal reaction, but are not intensely basophilic. Their failure to stain deeply with basic dyes and the fact that they never pass through a metaphase plate stage shows that they are not entirely homologous in their reactions to the metazoan chromosomes, but since they appear to be functionally identical they merit the term chromosome. Morris (1936) and Janicki (1909) also use the term chromosome for these structures (Text Fig. II).

Chromosomal strands.—Slender strands of discrete granules which appear in the central ground-plasm during early division stages. They appear to be the anlage of the chromosomes (Fig. 25).

Endosomes.—Large basophilic bodies lying between the peripheral and central regions. The question of their relation to nucleolar substance is discussed elsewhere. They have been termed pseudochromosomes (Morris, 1936, and Mercier (?) 1910). Kirby (1927) terms similar structures in amoebae from termites nucleoli (Text Fig. I).

Endosomal anlage.—The elongate heterophilic strands from which the endosomes develop during early interphase. They appear during very late telophase (Figs. 1, 2, 3; see p. 132).

Endosomal spherules.—The small spherules of basophilic material found in dividing nuclei. They occupy the median part of the constricting nuclei and are frequently arranged in irregular rows (Text Fig. II).

Hyaline body.—The mass of hyaline material lying at the poles of late kinetophase and early interphase nuclei, associated with the dedifferentiating chromosomes. This structure seems to be distinctive, no such nuclear element being described in other parasitic amoebae. It appears to be identical with the karyosome of Janicki (1909) (Figs. 9, 10).

Interphase.—The metabolic period during which no reaction with the Feulgen reagents can be demonstrated, indicating that there is no free thymo-nucleic acid, or that it is present in but very small amounts.

Kinetophase.—The division period. Lack of a metaphase makes it inadvisable to attempt to differentiate prophase and anaphase, so the whole division period is considered together under the term kinetophase. Early kinetophase signifies the period before the typical concentric arrangement of the nuclear elements is disrupted. Late kinetophase signifies the

period following the clumping of the chromosomes at the poles of the nucleus. Middle kinetophase refers to the period between these two stages. The kinetophase is considered as completed when the reaction to the Feulgen reagents is no longer demonstrable.

Peripheral granules.—The basophilic granules lying in the peripheral ground-plasm between the nuclear membrane and the endosomes (Text Fig. I).

Peripheral ground-plasm.—The ground substance between the endosomes and the nuclear membrane, containing the peripheral granules and peripheral spherules (Text Fig. I).

Peripheral spherules.—The refractive spheres which lie in the peripheral ground-plasm in living nuclei. They are resistant to staining with acid or basic dyes (Text Figs. I and II).

Peripheral zone.—The region between the nuclear membrane and the endosomes (Text Fig. I).

VIII. THE TROPHIC NUCLEUS; HISTORICAL REVIEW

A. INTERPHASE

Nuclear membrane.—The unusually heavy nuclear membrane is reported by all investigators as measuring from 1 to 2 μ in thickness. A refractive, homogeneous structure is described by these investigators for both living and fixed nuclear membranes. Bütschli (1878), who gave the first description of *E. blattae* from living material, described a delicate membrane which invested the nuclear membrane, separating it from the cytoplasm. This has never been confirmed. According to Schubotz (1905) the nuclear membrane appears to be bilamellar in some cases. He observed a dead organism in which the membrane had separated into a thin inner and heavier outer layer. This is unconfirmed by later workers. A distinct beak-like projection has been seen protruding from the nucleus by all the previous investigators. Janicki (1909) observed that the membrane is thinner at that point. Although no one has since definitely confirmed this, the illustrations in several publications by others have shown clearly that the projection has a thinner membrane than the remainder of the nucleus. No further contributions to the morphology of the nuclear membrane appeared until 1930, when Sassuchin reported that it had a striated structure in fixed and stained preparations. He believed that he could demonstrate a comparable physical structure in living nuclei studied with dark field illumination. These striations, he suggested, may represent a system of canals connecting the cytoplasm and the nucleoplasm. No investigator has confirmed his observations.

Peripheral zone.—Bütschli described the peripheral zone as a finely granular-reticular region. Schubotz (1905), who was the first to give a detailed account of the morphology of the nucleus in fixed and stained condition, made a careful search for nuclear structures and attempted to determine the nature of the elements he saw with artificial digestion experiments. He described the refractive peripheral spherules, whose rapid dissolution during artificial digestion led him to believe that they contained very little chromatin. The peripheral ground-plasm appeared as an orange reticulum, bearing a large number of orange granules when stained by the Flemming tricolor technique. Elmassian (1909) considered the peripheral reticulum as a continuation of the central reticulum. The refractive peripheral spherules, according to this investigator, were of a plasto-chromatin nature and were identical with the basophilic granules which he found imbedded in the reticulum of the fixed and stained nuclei. Janicki (1909), on the other hand, reported that the peripheral spherules were completely dissolved during the preparation of balsam mounts, unless dehydration was extremely rapid, when they were but partly dissolved. He was of the opinion that the spherules represented reserve food material for the nuclear elements. In 1910 Mercier observed that the granules comprising the peripheral zone were uniform in size. Kudo (1926) reported that the refractive spherules were of more or less uniform dimensions. They were resistant to staining with Lugol's solution, methylene blue, neutral red, Bismarck brown, and osmic acid. They disappeared on fixation, being replaced by a fine reticulum to which chromatin granules were attached. Morris (1936) described the peripheral zone as granular in the living and fibrous in the fixed state. He says (p. 232), "The peripheral zone contains granules which are highly refractive in living and chromatic in the fixed state." In this interpretation he agrees with Elmassian and disagrees with Janicki and Kudo. Sassuchin (1936) observed that the peripheral granules could be divided into two groups depending on their reactions to stains. Whether or not he means here that the spherules can be distinguished, or that the granules are of two kinds is not clear. At times during the life cycle the peripheral granules were found by Sassuchin to disappear.

Endosomes.—According to Schubotz (1905) there were a number of bodies, varying in size, shape, and number, which lay between the peripheral and central zones. They were not always visible in living nuclei. Spherical in shape, they measured from 2 to 5 μ in diameter. In Flemming triple preparations they were stained a light red. The rapid destruction of the endosomes during artificial digestion experiments indicated a small chromatin content. According to Elmassian (1909) the endosomes were composed partly of chromatin and partly of plastin. He

observed the very considerable variations in the shapes of the endosomes and attributed it to active movements of the nucleus. Janicki, in the same year, expressed the opinion that the endosomes underwent a growth period during the interphase, when chromatin material originating in the central region was deposited on them. In larger endosomes Janicki found transparent vacuoles. Kudo (1926) found the endosomes to be irregular in outline and usually more or less rounded. They were less basophilic than the peripheral granules. Sassuchin (1930) contended that the endosomes were nucleolar in nature. Morris (1936) observed that the endosomes were formed during the early interphase from the peripheral chromatin granules. He described them as hollow bodies with a more lightly-staining core and a more basophilic shell. In number they approximated the number of chromosomes, varying between 12 and 18 or more. The endosomes were destroyed during the late interphase, forming many small spheres and granules. Sassuchin (1936) observed that the endosomes varied a great deal in number, size, and structure, sometimes appearing to be spherical, sometimes oval, and again composed of a series of small spherules.

Central region.—The central region was first described by Bütschli (1878) as a cavity, probably filled with liquid, which sometimes contained a dark body. Schubotz (1905, p. 18) stated, "Schon an frischen Kernen lässt sich in diesen Centrum bei starker Vergrössung ein feines Wabenwerk wahrnehmen." The central region was a weak gray or yellow in Flemming triple preparations. During the course of his artificial digestion experiments almost everything in the nucleus was dissolved by the reagents except a few granules grouped in the center of the nucleus. These granules were specifically stained by Delafield's haematoxylin, and were all of the chromatin in the nucleus, according to Schubotz. Diametrically opposed to this opinion was that of Elmassian (1909), who considered the peripheral and central ground-plasms as continuous, and composed entirely of achromatic material. Janicki (1909) described the central region as an area containing many delicate granules, which he believed to be chromatic in nature. He also mentioned an eccentric karyosome which lay in the central region, and, according to his illustrations, was comparatively large in size. Mercier (1910) disputed the presence of a karyosome. Kudo (1926) found that the central region was more coarsely reticular than the peripheral zone, and was usually lacking in chromatin granules. No karyosome such as that described by Janicki could be found, but he did see an occasional small basophilic granule in the center of the central region, surrounded by achromatic substance. Sassuchin (1930) believed that he could see the karyosome described by Janicki in the living nucleus. Morris (1936, p. 232) states,

"Within this granular (peripheral) zone is a central reticulum which is clear in the living and densely reticular in the fixed nuclei, and in which a dot-like karyosome may sometimes be seen." This karyosome is not identical with the structure of that name described by Janicki, but appears to be the same as the central granule mentioned by Kudo. Sassuchin (1930) describes a cellular structure for the central region. A karyosome was found in some nuclei. This structure, also, appears to be identical with the central granule of Kudo.

B. KINETOPHASE

Mercier (1908-1910) was one of the first to give an account of karyokinesis in *E. blattae*. According to his observations the first indication of approaching nuclear division was the destruction of the endosomes and the formation of a number of fine chromatic granules. These were arranged in a longitudinal series on an achromatic ribbon which was formed in the central region. From the long beaded strand a more or less homogeneous ribbon which was uniformly basophilic was developed. Until this time there were no visible changes in the rest of the nucleus. Through fragmentation of the long "spireme" 4, 5, or 6 pseudochromosomes were formed. Because of the variation in number of these structures, Mercier came to believe that they could not be true chromosomes, hence his term pseudochromosome. As these pseudochromosomes began to migrate toward the poles the nucleus began to elongate. Ultimately a constriction across the longitudinal axis separated the two daughter nuclei. During reconstruction after division the pseudochromosomes became clumped in the center of the nucleus forming a reticulum from which the endosomes were derived.

Elmassian (1909, p. 52) remarked concerning the description of division offered by Mercier, "D'après cette description il nous es difficile de voir la un division mitotique, il s'agit tout simplement d'un changement du noyaux dan lequel les quelques variations de la chromatine ne sont peut-etre autre chose que la modification du noyaux au stade végétatif dont il a été question plus haute." Thus relegating Mercier's observations to changes in the interphase, Elmassian described the reconstruction of the nucleus immediately after division. This was the only stage of karyokinesis that he had seen. In the recently divided nuclei the membrane was appreciably thinner than usual. The whole nucleus was at first filled with fine chromatic granules which gradually aggregated to form the definitive endosomes.

Janicki (1909) offered a contrasting interpretation of karyokinesis. He believed that he had seen two kinds of division. An amitotic type division involved elongation of the karyosome and its subsequent division,

followed by a simple constriction of the nucleus, dividing the peripheral zone and central region into two parts. Elongation of the karyosome likewise initiated mitotic division. It first elongated at right angles to the long axis of the nucleus and later rotated through 90 degrees to coincide with the nuclear axis. A spindle was formed from the karyosomal material. There were more than 6 chromosomes which migrated to the poles of the nucleus without going through an equatorial plate stage. At anaphase they became arranged at the poles of the constricting nucleus, where they formed a rosette, surrounded by transparent karyolymph. The polar clump of dedifferentiating chromosomes became twisted and irregular and finally formed a mass of chromatin at the poles of the nucleus. Nuclear constriction was not completed until the chromosomes were at least partially dedifferentiated. Janicki reported that it required 15 minutes for nuclear constriction to occur in a dividing nucleus observed in life.

Kudo (1926), who, like Janicki, observed division in living and fixed amoebae, reported that just before division began the refractive peripheral spherules began to undergo a very marked Brownian movement. As the living nucleus elongated the clear central region also became oval, and then bilobed as the nuclear constriction began. The peripheral spherules were concentrated in the center of the nucleus as the clear central material migrated to the poles, where, as can be seen clearly in his figures, there remained a small area free from the spherules. This clear area appears to be the divided central region. A long intradesmose connected the two daughter nuclei until the constriction cut through it. One division required 10 minutes while another took 60. One was followed immediately by cytokinesis, and the other was not. In fixed and stained nuclei the early stages of division were characterized by an elongation of the central region and enlargement of the peripheral chromatin granules. These migrated toward the central region and formed several lines, extending from one pole to another, investing the central region. They appeared to increase in number, possibly by division, at this time. Then they were grouped in two masses which moved toward the two poles where they were linked together in rod-like structures. Nuclear constriction separated the two daughter nuclei, after which the chromatin bodies assumed a rounded compact form and were scattered over the achromatic network.

Morris (1936) described mitotic division for *E. blattae*. According to him the first indication of approaching division was the disruption of the typical concentric arrangement of the nucleus and destruction of the endosomes. This produced a sponge-like reticulum which carried chromatin in the form of net-knots. As the nucleus began to elongate

fine filiform chromosomes emerged from the reticulum. These were stained but lightly and were masked by the reticulum up to this time. As the chromosomes migrated to the poles, the nucleus continued to elongate. The chromosomes formed a clump at the poles as the constriction of the nucleus began, after which they became ragged and vesicular, losing their identity in the formation of a new central region. The chromatin spherules derived from the peripheral region were located at the antipolar end of the telophase nucleus, but migrated around the developing central region, thus reestablishing the concentric arrangement typical for the interphase nucleus.

IX. THE NUCLEUS IN LIFE

EVEN UNDER low magnifications the nucleus is very prominent in *E. blattae* because of its large size and highly refractive nuclear membrane. It is usually about 20 μ in diameter but may be appreciably larger in some cases. A number of nuclei between 20 and 25 μ in diameter were seen. The largest nucleus recorded in which no indication of parasitism or abnormalcy could be found was just over 30 μ in diameter. When parasitized by Nucleophaga or when undergoing degenerative changes the nucleus increases in size, sometimes reaching almost double normal size. During the early stages of the development of Nucleophaga the nucleus remains about normal (Fig. 56), but as the later stages are reached hypertrophy of the nucleus begins. The nucleus appears to reach an ultimate size of nearly twice its normal diameter.

The thickness of the nuclear membrane appears to vary from just less than 1 μ to about 2 μ . The delicate cytoplasmic membrane investing the nuclear membrane described by Bütschli (1878) was not seen. The most careful search for any indication of a bilamellar structure of the nuclear membrane such as that described by Schubotz (1905) has remained unsuccessful. In bright and dark field illumination the nuclear membrane remains clear and hyaline, without any sign of division. Occasionally one or several bright lines can be seen in bright field, but from their reactions to focussing and shifting of light they seemed to be diffraction images with no structural basis. A beak-like projection at one pole of the nucleus is common. This has been observed by all previous investigators, and generally interpreted as a remnant of the internuclear strand connecting daughter nuclei during division since Janicki (1909) first suggested this explanation. As Janicki observed, the membrane is thinner at this point. The projection appears to gradually decrease in size, with an accompanying increase in the thickness of the membrane. Ultimately it remains as a small, rounded prominence on the nuclear membrane.

The most conspicuous element of the peripheral zone is the large number of highly refractive peripheral spherules (Fig. 38) which are suspended in the almost transparent karyolymph. They vary greatly in size and number in different nuclei, but are comparatively uniform in size and regularly distributed in any one nucleus. The spherules are collected at one side of the nucleus in most cases. This appears to be the result of a slow migration of the spherules through the ground-plasm during nuclear reconstruction following division. Nuclei with the spherules distributed equally throughout the peripheral zone are quite rare. Observed in white light, the spherules have a slightly yellowish tinge. In bluish light they are greenish.

Kudo (1926) reported that the spherules were less numerous in small amoebae with little food in the cytoplasm than in large, well-fed specimens. The same tendency was noticed in the present study. This seems to be explained by the effects of early development leading ultimately to the precystic condition, to be discussed in greater detail subsequently. As the amoebae begin to approach encystment, the division rate increases, and the cytoplasm becomes increasingly clear as the food vacuoles and other included material become less abundant. As a result of the increase in rate of division, the peripheral material of the nucleus becomes greatly diminished (see p. 108). This is true, not only for the peripheral spherules, but for the ground-plasm and endosomes as well. The increase in division rate seems to be the factor most important in bringing about a reduction in the size of the amoebae as well. These facts lead the writer to the opinion that Kudo observed trophic amoebae which were approaching a precystic state. Janicki's suggestion that the peripheral spherules represent reserve food material for the nucleus might be supported by these observations were it not for the fact that the reduction of peripheral spherules seems to be a normal part of the development of precystic forms. It is still possible, of course, that the disappearance of the food vacuoles cuts off the supply of material from which the peripheral spherules are formed. Against this possibility some evidence may be adduced. A study of amoebae from starved cockroaches which contained no food vacuoles and had cytoplasm as clear and transparent as precystic amoebae showed no decrease in the number of peripheral spherules, nor in the size of those present, insofar as could be determined. At least in the larger trophic amoebae, then, the disappearance of food vacuoles is not associated with a decrease in the number or size of peripheral spherules.

Small, inconspicuous granules also occur in the peripheral zone. These bodies, from their distribution and size, appear to be identical with the basophilic peripheral granules. They are never distinct except in nuclei

in which the peripheral spherules are clumped at one side of the peripheral zone. In such cases the small granules can be seen clearly in the opposite side of the zone. Previous investigators have apparently failed to distinguish these granules in living amoebae. Once they have been seen, many of the contradictory statements concerning the staining reactions and relation of the peripheral spherules to the basophilic granules may be understood (see p. 85).

The ground-plasm in which the spherules and granules are suspended is normally in the gel phase, as is shown by the absence of Brownian movement in the peripheral granules. It is not easy to see in the living nucleus, and even in the most favorable conditions appears only as an indistinct outline. In nuclei with the peripheral spherules collected at one pole of the peripheral zone, the ground-plasm can sometimes be seen indistinctly at the other. In such nuclei, even though the substance of the ground-plasm cannot itself be seen, the distribution of the peripheral granules makes it possible to determine the outlines of the peripheral ground-plasm. No Brownian movement was observed in the peripheral granules when the nucleus was compressed, nor during the early degenerative processes occurring in free nuclei outside of the amoebae. Apparently solation of the peripheral ground-plasm occurs only during division.

Lying between the central region and the peripheral zone there is a girdle of large endosomes. These are but rarely visible in life, and, when seen appear as indistinct hyaline bodies without clear outlines. Attempts to determine the differences in nuclei in which the endosomes were visible in life have been unsuccessful so far.

Within the endosomes lies the clear, transparent central ground-plasm. According to Schubotz (1905) this region is reticular in living amoebae. Sassuchin (1936) also believed that he could demonstrate a cellular structure in the central region of living amoebae. The writer has been unable to confirm these reports. With the optical equipment used there was visible a pattern of bright lines through the center of the nucleus. These were visible only in areas covered by the peripheral spherules, and appeared to be produced by diffraction of light through the spherules. Dark field studies, likewise, failed to reveal a reticular structure.

Stages of late nuclear reconstruction were studied in life. At this time the Brownian movement of the peripheral spherules described by Kudo had ceased, and the peripheral region had an uneven distribution of the various elements. The spherules were clumped at one pole, and very gradually moved around the central region. This was the only change that could be followed in life in the material studied.

X. NUCLEAR ACTIVITIES DURING THE TROPHIC STAGE

It is not easy to determine which structures are artifacts and which are truly reflections of structures present in the living nucleus in the case of *E. blattae*. The large number of nuclear elements, some of which are invisible in life but visible in the fixed nuclei and others of which are visible in living nuclei but usually absent in fixed nuclei, serve to complicate the problem. In the following account of the nuclear appearance and nuclear changes during interphase and kinetophase the interpretations made are not explained in all cases. All interpretations were based on the study of the effects of fixatives on the nucleus, and the bases for them are treated in subsequent sections. Detailed and exhaustive accounts of slight variations in appearance due to fixation and staining are not given here. These, too, can be found in succeeding sections. This discussion, then, represents the generalized sum total of the experiences of the writer, critically considered, with the view of describing and interpreting the nuclear activities of the trophic amoeba.

A. THE INTERPHASE

In the nuclei of most organisms the interphase condition is a morphologically static stage during which the metabolic activities are carried out with a minimum of visible changes. The chromatin remains in a dispersed state throughout the interphase, or is centered in a definite endosomal body with a greater or lesser amount scattered between the endosome and the nuclear membrane. This appears to be quite unlike the condition in *E. blattae*. Definite morphological alterations accompany the interphase nuclear activities. When the division rate is high the nucleus has an appearance distinctly unlike that observed in cases where the division rate is low. In hosts in which a large number of division figures were found interphase reorganization was restricted. When the division rate is low the nuclei remain in the interphase condition for a relatively long period of time, and the organization and appearance of the nucleus reflect the long duration of the metabolic activities without nuclear reorganization.

The interphase proper begins when the migration of peripheral elements around the central region produces a continuous peripheral zone around the central chromosomal material, which is at this time negative to the Feulgen reaction. The central region is granular, and in some cases contains a few indications of the old dedifferentiating chromosomes. The endosomes are present as series of basophilic granules or spherules connected by a lighter-staining substance, or as discrete small spherules. The

ground-plasm is filled with a large number of peripheral spherules and granules. The spherules remain clumped at one pole of the nucleus, while the granules are more or less equally distributed throughout the whole peripheral ground-plasm (Fig. 4).

The reorganization of the central region during early interphase entails the disappearance of granules associated with the chromosomes, an almost complete loss of affinity for basic dyes, and a loss of the positive reaction to the Feulgen nucleal test. At the late kinetophase period, the chromosomes are found in a clump at one end of the nucleus, more or less fused together, and already partially or almost wholly lacking in basophilic material (Figs. 1, 2). Nuclei, unless fixed with Flemming, do not show a hyaline body. After Flemming fixation, however, a hyaline body may be found (Fig. 4). This structure, becoming less basophilic as the interphase advances, is characterized by its constant polar position adhering to the central region, and its clear hyaline appearance. It remains for part of the interphase period (Fig. 15). The central region gradually comes to occupy a position in the center of the nucleus, migrating slowly from the pole as the peripheral ground-plasm, carrying peripheral granules with it, moves down and around it. Apparently the central ground-plasm, during this period of development, is unusually dispersed, for it is usually shrunk more during fixation than at later stages, drawing away from the peripheral ground-plasm to a marked degree (cf. Figs. 4 and 9). After the central region has come to occupy a central position, or is approaching it, the central and peripheral ground-plasms usually are connected by radii-like strands of the central ground-plasm (Figs. 5, 6), unless fixed in a fixative which entails little or no shrinkage of the ground-plasm, in which case it is attached to the peripheral region along its whole margin (Figs. 9, 10). The hyaline body is at first slightly basophilic, but as the peripheral material gradually invests the central material the hyaline body becomes less basophilic and stains rather deeply with the acid dyes. Shortly after the central ground-plasm has attained its final appearance and is no longer colored by the Feulgen reaction, the hyaline body disappears, to be seen no more until the late kinetophase of the next division. Insofar as the central ground-plasm is concerned, there are no marked changes in its appearance from this time until the chromosomes begin to appear during the following division. It is at this time either a reticular or amorphous region of acidophilic material, which is occasionally found to contain small granules of more intensely acidophilic substance, especially after fixation in Gilson-Carnoy. Attempts to correlate the appearance of these granules with endosomal appearance have, thus far, been unsuccessful.

At the time that the central ground-plasm is forming in the chromo-

somal clump at the pole of the nucleus, the peripheral ground-plasm, migrating along the nuclear membrane to the pole of the nucleus, contains the deeply basophilic endosomal bodies and the peripheral granules, slightly less basophilic. Ultimately a more or less even coating of the nuclear membrane is formed, and from this time on the peripheral ground-plasm retains its structure and appearance. It is usually reticular, especially after the less vigorous fixatives, but occasionally develops an odd fibrous appearance (Fig. 14), in which the alveolar walls tend to be stretched at right angles to the nuclear membrane. The endosomes likewise tend to become more evenly distributed around the central ground-plasm, but the peripheral spherules lag behind the other peripheral elements, usually retaining their uneven distribution until the next division. Nuclei in which the peripheral spherules are evenly distributed are extremely rare.

Once the typical concentric arrangement of the various nuclear parts has appeared, with the central ground-plasm occupying a central position, surrounded by a sub-equal layer of the peripheral ground-plasm containing spherules and endosomes more or less equally distributed throughout, very little change occurs in the nuclear elements, exclusive of the endosomes, until the next division. These undergo a series of gradual changes which comprise the most striking feature of interphase activities. In the early interphase there is a great diversity of appearance in the endosomal material which appears to be reflected in later stages. The diversity of appearance is such that there can be no doubt that the endosomal changes do not follow a rigid course of development. The variation in endosomal appearance in late interphase stages appears not to be a random one, however, and the writer believes that there is a seriation of indefinite morphological types.

The endosomal development begins during the late kinetophase. At this time endosomal anlage are formed from basophilic endosomal spherules derived from the endosomal substance of the parent nucleus during the early kinetophase stage (Figs. 1, 2, 3). The endosomal anlage appear as strands of endosomal spherules, which are connected by a more lightly-staining substance. Not all of the spherules are fused to form the endosomal anlage at this time, however, and a greater or smaller number of them remain as discrete bodies at the pole of the nucleus lying opposite to the dedifferentiating chromosomes. At first the endosomal anlage tend to lie in straight lines, but after the peripheral ground-plasm has finished its migration around the central region, the endosomal anlage assume characteristic sinuous shapes (Figs. 7, 12). The original beaded appearance of the endosomal strands gradually disappears and the endosomes appear as winding bars of deeply basophilic material. In nuclei

which have undergone a greater amount of differentiation after staining, however, the spherules composing the anlage can still be seen (Figs. 5, 9, 11). The spherules are more distinct in nuclei which have been stained with safranin than in nuclei which have been stained with haematoxylin in these later stages, unless differentiation is carried far beyond the normal point. This indicates that the lighter-staining substance which originally connected the endosomal spherules develops an affinity for haematoxylin at a more rapid rate than it develops an affinity for safranin. The endosomes later lose their beaded appearance even when destaining is almost complete, and at this time show a definite tendency to become shorter and heavier (Fig. 13). During this stage of their development the resemblance of the endosomes to metaphase or late prophase chromosomes of metazoan nuclei is very striking, which probably accounts for the term pseudochromosome which has been used by Mercier (1910) and Morris (1936) to indicate these middle interphase endosomes. It is interesting to observe that the endosomes tend to assume angular shapes after Gilson-Carnoy fixation (Fig. 16), but tend to be spherical after Schaudinn or Flemming fixation (Fig. 17). Zenker fixation, likewise, favors the spherical shape. It appears that most nuclei do not progress beyond this stage but undergo a division before later developments occur. This, then, is the typical interphase condition (Figs. 15, 16). If the division rate is extremely low, later endosomal changes may occur. To what extent these are degenerative and to what extent normal is not known at this time. The endosomes become larger and develop a vacuolated appearance. Even in the middle interphase condition a differentiation of a cortical deep-staining and an inner lightly-staining portion is frequently observed, but in these very late stages the endosomes show this characteristic even more clearly (Fig. 18), and a small central granule of basophilic material can be seen. It is not uncommon for the lightly-staining material in the endosome to become distributed in small vacuoles during further development, which entails a reduction in the number of endosomes and an increase in size. It was thought that this might be an indication of the beginning of the disintegration of the endosomes preparatory to the next division, but since most nuclei divide long before this stage is reached, it seems improbable that it is a regular occurrence.

In one host, especially, and more rarely in several other hosts, the endosomes were sometimes found in a very characteristic orientation. Endosomes in the short rod condition, approaching the cuboidal shape, became arranged in a more or less parallel pattern forming a girdle of endosomes about the nucleus (Fig. 13). The significance of this type of development is not known.

This endosomal development has not entirely escaped the attention of

earlier investigators. Mercier (1910) described part of this process (see p. 34). The process involved, as he described it, the formation of beaded strands which became homogeneously basophilic and assumed sinuous shapes. These strands formed a spireme thread which broke up into pseudochromosomes. The writer has observed several nuclei in which the endosomal substance was almost entirely gathered in one long sinuous endosome. Mercier reported that there were usually from 4 to 6 pseudochromosomes. In the material used for this study there were usually a dozen or more. This may be an indication of a racial difference in the materials studied. At the present time there is no information on the variations which occur in *E. blattae* in different species of cockroaches growing under various environmental conditions, so that no positive evidence can be adduced for this point. The later stages of division described by Mercier are not very clear. Amoebae have occasionally been found which resemble certain of his figures, but it is not as yet completely understood. This might, again, be associated with racial, environmental, or host differences. Mercier, then, has described some of the steps in the development of the endosomes during the interphase, although he believed that they were a part of the division phenomena.

Earlier work of Mercier (1907, 1909) in which the same division cycle was described in practically the same words brought forth a comment from Elmassian (1909) that he believed it probable that Mercier had observed vegetative rather than division phenomena (see p. 34). Elmassian appears to have noted some of the endosomal changes mentioned and interpreted them as vegetative in nature. He is thus the first to hint at interphase nuclear changes. Janicki (1909) also mentioned endosomal variation and described the growth of the endosomes during interphase. Morris (1936, p. 233) mentions the variation in endosomal appearance and says, "They exhibit a gradual change, from late telophase to early prophase, seeming to alternate in period of activity with the true chromosomes." Unfortunately he does not elaborate on this statement insofar as the changes he had noticed are concerned.

The endosomal activity is quite unlike that found in most of the other members of the genus *Endamoeba*. In the *Endamoeba* described by Kirby (1927) from termites a more or less similar nuclear appearance during interphase was noticed, although he did not describe any trends of endosomal changes similar to those mentioned here. Most striking was the occurrence of the elongate sinuous endosomes in *E. disparata*, very similar in all respects to those found in *E. blattae*. In *Euglypha* sp. Bělař (1926) described endosomes which were, in many respects, similar to the elongated endosomes found in *E. blattae*. These, however, lay in the center of the nucleus instead of the periphery. They were broken

down during early division stages, and the chromosomes were formed from peripheral material and not from endosomal material. This appears to be a case in which the arrangement of the nuclear material is the exact reverse of that observed in *E. blattae*, although the conditions appear to be analogous in most respects.

The functional significance of the endosomal alteration during interphase is not understood completely. The changes suggest that the endosomes may be extremely active during the metabolic period. Morris (1936, p. 245) has considered the possibility that the peripheral chromatin of *E. blattae* represents trophochromatin. He says: "A plausible explanation of the behavior of the peripheral chromatin of the adult *E. blattae* is not easy to reach. Its apparent quiescence during the mitotic portion of the nuclear cycle and notable activity during the interphase seem to set this species in a group by itself. The nearest approach to this phenomenon appears to be the case of the opalinid, *Zelleriella*, described recently by Chen (1932), but even this does not present a perfect analogy. Metcalf (1909) and, later Tönniges (1919) and Bélař (1926) suggested the similarity of the large chromatic bodies in the opalinid nucleus to the macronuclear material of such infusoria as *Paramecium*, and this may well be so, regardless of the fact that these writers failed to describe the chromosomes correctly and therefore misinterpreted much of what they saw.

"If the same analogy holds true for the trophochromatin of *E. blattae*, although this must still be considered hypothetical, then it may well be that the peripheral chromatin of all the Endamoebae should be considered in this way, for the pseudochromosomes of *E. blattae* give every indication of being homologous to the trophochromatin of other members of the genus."

The writer wishes to subscribe to the opinion of Morris. As will be seen in later sections of this study, there is a great difference in the staining reactions of the peripheral and central "chromatin" of the nucleus of *E. blattae*. This, with the difference in their reaction with fixatives, appears to indicate definite chemical differences (see p. 87 ff.). It is probable, although yet hypothetical, that the endosomes contain a nucleoprotein, while the central region contains, at division stages, nucleic acid, and during the interphase a nucleoprotein, which, in chemical composition or in physical state, is distinct from the nucleoprotein of the endosomes. The paradoxical situation in which the most prominently basophilic nuclear elements, the endosomes, do not show a direct genetic relationship to the chromosomes is not unlike the situation in *Amoeba proteus* as described by Chalkley (1936). At the present time no definite conclusions can be drawn, but it becomes increasingly possible that, as in the ciliates,

there is a segregation of trophic and kinetic chromatin which may express itself in the nuclear structure of the organisms and in the relationship of the nuclear elements composed of "chromatin" to the true chromosomes.

B. THE KINETOPHASE

Kinetophase changes may begin at any point in the interphase cycle, depending on the division rate. The chromosomal cycle appears to be the same, regardless of the division rate, but the activities of the peripheral material depends to a certain extent on the length of the interphase preceding the division and the appearance of the endosomes at the time division begins.

The central region of the late interphase nucleus is composed of a reticular or homogeneous region in permanent mounts, in the center of which a centriole can be seen in many nuclei. At this time the ground-plasm is more or less acidophilic, depending to some extent on the fixative, and invariably negative to the Feulgen nucleal test. The first noticeable step towards division is observable in the central region, which becomes somewhat more reticular, and begins to show slight affinities for the basic dyes. At this time a slight tint of violet is observed in nuclei subjected to the Feulgen reaction. This positive reaction with the Feulgen reagents occurs diffusely in the whole ground-plasm of the central region. This is followed by the appearance of delicate granules, which are especially well demonstrated after fixation in Gilson-Carnoy and Flemming (Figs. 20, 21). These granules appear to be more basophilic than the surrounding ground-plasm, and in rare instances seemed to be more intensely colored by the Feulgen reaction than the ground-plasm. This last observation is not made with a great degree of certainty, however, as the reaction is too light at this time to make comparisons certain. The granules are soon afterwards arranged on strands which lie twisted and coiled together in the mass of central ground-plasm, which, at this time, becomes noticeably smaller in amount. These strands, like the granules, show a greater affinity for basic dyes than does the surrounding ground-plasm and appear to react more intensively with the Feulgen reagents. The strands assume a beaded appearance as the granules are collected along them. At this time the centriole, when visible, is double (Fig. 21). It is at this time that the nucleus suddenly enters into a "dedifferentiated phase" which disrupts the normal concentric arrangement of the nuclear elements. The peripheral material is greatly altered in appearance as the ground-plasm becomes very irregular in distribution, and the endosomes are broken down into small spherules (Figs. 22, 23). At this time it becomes impossible to differentiate the central region, and the whole nucleus becomes filled with a

spongy mass of material with the endosomal substance distributed at random throughout the nucleus. This period appears to coincide with the period of active Brownian movement described by Kudo (1926), who watched living nuclei in the process of division. The endosomal spherules and the peripheral ground-plasm gradually come to occupy the central part of the nucleus, investing the central region, which becomes visible once again beneath the girdle of peripheral material (Figs. 24, 25, 26). The central region is now distinctly elongated or bilobed, and the chromosomal strands are much more distinct, while the centrioles show a distinct tendency to be much farther apart than before the "dedifferentiated phase." The nucleus is usually beginning to elongate at this time. The most careful search has failed to show any stage comparable to a metaphase. As soon as the peripheral material has arranged itself in a girdle about the central part of the nucleus, the chromosomes, still twisted and coiled, begin to migrate toward the poles, and appear protruding from the edges of the peripheral girdle. The central ground-plasm is not entirely gone at this point, and usually assumes a bilobed appearance during the first part of the migration. It is during this migration that the chromosomes undergo their final development and appear as homogeneous strands, or, in some cases, as comparatively heavy strands of light-staining substance containing small granules of basophilic material in them. As the nucleus begins to constrict, or, sometimes, before constriction begins (Figs. 27, 28, 29) the chromosomes have completed their migration to the poles, and may be seen in a rosette at the poles of the nucleus. During the last portion of their movement to the pole they assume a characteristic V-shape, similar to that of chromosomes during anaphase in metazoan mitosis. At this time they react very distinctly to the Feulgen technique, and show some affinity for basic dyes. The endosomal substance, gathered in small spherules after the "dedifferentiated phase," remains very intensely basophilic, much more so than the chromosomes, but does not react with the Feulgen reagents. Nuclear constriction appears to occur rather more slowly than the changes preceding it, and long intradesmoses sometimes persist for some time after division appears to be complete in other respects. As the nucleus constricts, and the chromosomes reach their polar position, the peripheral material comes to occupy the center of the elongated nucleus. The endosomal spherules and the refractive peripheral spherules tend to lie in straight lines at this time (Fig. 29), although the linear arrangement is frequently quite irregular, and at least partially disrupted by the tendency of the endosomal spherules to form a coarse reticulum (Fig. 30). The spherules of refractive substance so characteristic of the living nucleus cannot be studied advantageously in permanent mounts made

from material fixed with compound fixatives, but were observed in amoebae fixed with formalin. In these nuclei the tendency of the peripheral spherules to lie in straight lines during the constriction of the nucleus was very marked, even more so than was the case with the endosomal spherules. After nuclear constriction is complete the two daughter nuclei reorganize themselves into typical interphase nuclei.

During the reorganization of the interphase nuclei from the daughter nuclei, the endosomal spherules form in lines, and become connected by a light-staining substance, described with the interphase nucleus. These endosomal anlage gradually become homogeneous in their staining reactions, and migrate with the peripheral ground-plasm about the central region, which gradually comes to assume its definitive central position.

In safranin, particularly, the chromosomes appear as a row of basophilic granules arranged on an acidophilic strand. The granules are conspicuous during the time that they form a rosette at the poles (Fig. 28), but as the interphase reorganization occurs the granules become less prominent and ultimately disappear entirely. As the clump of chromosomes begins to undergo its transition into the central region, a mass of hyaline material appears at the pole of the nucleus. This is quite basophilic at the time that the granules are visible (Fig. 4), but afterwards gradually loses its affinity for basic dyes, and ultimately stains almost exclusively with the acid dyes. As the hyaline body appears, the chromosomes fuse together, lose their individuality insofar as can be determined visually, and form the central ground-plasm of the daughter nuclei.

The endosomal material lying in the constricted region of the new daughter nucleus is less easily followed. The endosomes are destroyed in the early kinetophase, and are not present as such during division. In their place a large number of small endosomal spherules are found. The method of endosomal destruction and the relationship of the old and new endosomes to the endosomal spherules appears to have been a source of much difficulty in descriptions of the division of *E. blattae*.

Kudo (1926, p. 147) says, "When the nucleus starts to divide the chromatin granules become larger in number and size. . . . The chromatin granules become grouped into a number of somewhat larger bodies, spherical or rounded-oval, which become arranged in several lines between the poles over the achromatic reticulum." This would indicate that there was a fusion of the peripheral granules to form the endosomal spherules. Morris (1936, p. 233) differs in his interpretation, saying, "They (the late interphase endosomes) appear to be hollow, or composed of lightly-staining material surrounded by a more heavily-staining zone. This condition terminates with a breakdown into spheres and granules as

the prophase approaches." Earlier he says (p. 233), "During the late telophase-early interphase period the granules of peripheral chromatin are usually in the form of connected series like strings of beads. These coalesce to form large chromosome-like bodies or pseudochromosomes, intermingled with small dense chromatic granules." The relationship of the material formed from the old endosomes to the new endosomes is not made clear. If the peripheral chromatin granules form the new endosomes, the fate of the old endosomal material is still unexplained.

Certainly the two most probable methods of endosomal disruption are gradual disintegration by vacuolization and loss of basophilic material, or disruption into endosomal spherules directly. During the late interphase period the endosomes are fewer in number and larger in size. These larger endosomes are vacuolated, and in some cases show by irregular contours that they may be produced by fusion of smaller elements. The development of vacuoles may possibly be taken as a sign of loss of basophilic material by slow dissolution or chemical change resulting from use. Fusion in itself may be a sign of early disintegration. In some of the larger endosomes there is no sign of fusion, indicating that the endosomes may have grown directly before beginning, or while in the process of, vacuolation. These observations seem to indicate that the destruction of the old endosomes simultaneously involves fusion, vacuolation, and dissolution of the basophilic material. On the other hand the nuclei found in hosts showing a high division rate show no indication of vacuolation of endosomes. In such nuclei the endosomes seem to break down directly into smaller basophilic elements, and since they appear at this time, the endosomal spherules are the most probable products. Indeed, during the early kinetophase "dedifferentiated stage," the formation of the spherules from endosomes can be seen directly. A combination of the two methods, with the emphasis on vacuolation when the division rate is low, and on a general physical disruption when the rate is high, seems to be the most satisfactory explanation with the data now at hand.

In case the endosomal material is largely dissolved the endosomal spherules of the dividing nucleus must be developed from some existing nuclear element other than the endosomes. This seems to devolve on the peripheral granules, which, as Kudo says, increase in size and become grouped together to form the larger spherules. It has not been possible to demonstrate fusion of the peripheral granules, and to what extent they enter into the formation of endosomal spherules has not yet been determined.

Once the endosomes have disintegrated and the endosomal spherules have formed, the nucleus enters the so-called "dedifferentiated phase."

This is characterized by the coarse reticulum carrying a large number of basophilic elements, completely surrounding and obscuring the central region. The probable significance of this has never been completely understood. Morris suggests, and with the probability of being correct, that it is associated with the Brownian movement of the peripheral spherules observed by Kudo during division of living nuclei. The fact that the reticulum formed by the peripheral ground-plasm is so irregular at this time may possibly indicate that there has been a shift from gel to sol phase in the material comprising the peripheral region.

The spherules then become arranged in rows extending from pole to pole of the elongating nucleus, as described by Kudo. These rows are superficial, lying around the central region, as can be plainly seen in rare favorable cases where the peripheral material does not wholly obscure the central region (Figs. 25, 26). The constriction of the nucleus divides the endosomal spherules between the two daughter nuclei, but there is no indication of a true quantitative division. No mechanism for accomplishing an even distribution has been found, unless the tendency toward forming rows, extending almost from one pole of the constricting nucleus to the other, be considered as having this function.

The breakdown of the endosomal substance and the formation of new endosomes with each division of the nucleus is an extremely interesting phenomenon. If the peripheral basophilic material is considered as trophochromatin, it acquires some significance. In the macronucleus of several ciliates reorganization bands have been described. Turner (1930), Kidder (1933), and Summers (1935), for example, have described such phenomena in *Euplotes patella*, *Conchophthirius mytili*, and *Aspidisca lynceus* respectively. Occasionally this is accompanied by the discarding of a part of the macronuclear chromatin, as described by Kidder for *Conchophthirius*. This may be paralleled in *Endamoeba blattae*, as Kudo (1926, 1939) points out. In the division of a living nucleus Kudo observed the formation of a small bulb in the connecting strand, which may be compared to the chromatin cast out of the macronucleus of *Conchophthirius*. The writer has observed similar bulges in the connecting strand extending to daughter nuclei in fixed preparations. How frequently or regularly they occur is not yet known, but it seems certain that they are not of universal occurrence, for in many division figures the bulb is wholly lacking.

The parallelism of the endosomal changes of *E. blattae* and the macronuclear changes of these ciliates is in many ways most striking. The ciliate reorganization band appears to involve a shift from gel to sol phase in the region of the clear solution plane. In *E. blattae* there is a shift from gel to sol phase in the peripheral ground-plasm, which

apparently accompanies the breaking up of the endosomes. The bulb is composed entirely of peripheral material, since the peripheral material comes to occupy the central part of the constricting nucleus. Thus the endosomal material must be represented in the discarded material, and appears in it in fixed preparations. But the significance of this parallelism cannot be determined at the present time. The mechanisms involved are quite dissimilar. In addition, there is some uncertainty which we necessarily feel concerning the question of whether the endosomal substance can be reasonably called trophochromatin, at least in the same sense as can the ciliate macronucleus. The writer, however, does wish to emphasize the fact that the parallelism in the activities of the peripheral chromatin of *E. blattae* and macronuclear organization of some ciliates serves to support, in some degree, the idea that the peripheral chromatin of *E. blattae* may be a type of trophochromatin.

When the constriction is completed the daughter nuclei have a very characteristic appearance (Fig. 31). At the pole lie a number of chromosomes in the form of a rosette. The whole antipolar region is packed with the endosomal spherules and the peripheral spherules, which, like the former, were passively distributed to the two daughter nuclei in about equal numbers. The concentric arrangement is restored by the migration of the peripheral material about the developing central region. The endosomal spherules begin to fuse together during this migration, forming the endosomal anlage (Figs. 1, 2, 3), composed of the intensely basophilic endosomal spherules connected by strands of more lightly-staining material. The endosomal material sometimes appears to precede the peripheral ground-plasm in the migration about the central region. As the ground-plasm reaches the polar end of the nucleus, completely investing the central region, which, by this time, has completely or almost completely lost its ability to react with the Feulgen reagents, the interphase begins.

Formation of new endosomes appears to involve a fusion of the endosomal spherules rather than the peripheral granules, as suggested by Morris. The early endosomal anlage appear to be composed of basophilic structures too large to be identified as peripheral granules, and more basophilic than the granules. Indeed, it is possible to decolorize the granules entirely, while leaving the endosomal spherules still quite deeply stained (Fig. 5). It seems possible that at least some of the endosomal spherules are partly formed from the peripheral granules during the early division stages, and also that the gradual development of a homogeneous staining reaction in the endosomal anlage entails an accumulation of the peripheral granules in the lightly-staining portion of the anlage, but this has not been definitely demonstrated. It is certain, how-

ever, that there is an increased amount of basophilic material in the endosomes, developed during early interphase, which may quite possibly arise from the lightly-staining substance composing the connecting strands of the anlage, or may be obtained from the peripheral granules.

Division, as it occurs in *E. blattae*, is quite unlike that described for *Entamoeba histolytica* by Kofoed and Swezy (1925) or by previous investigators for that species. The work of Cleveland and Saunders (1930) only serves to make the difference between these two species of amoebae even more striking. The close similarity of the division of the termite Endamoebae, *E. disparata* and *E. simulans*, described by Kirby (1927) supports the idea that these organisms are very closely related and are rather distantly related to other forms of parasitic amoebae.

The termite amoebae and *E. blattae* present a very characteristic type of division, entailing the absence of a metaphase plate, and the presence of a comparatively large number of chromosomes which appear in the center of the nucleus as beaded strands. Kirby did not use the Feulgen reaction, so that the question as to whether or not there is a variation in the demonstrable nucleic acid of the nucleus of *E. disparata* or *E. simulans* during division, similar to that observed in *E. blattae*, is not known. The activities of the endosomes during division are similar in these forms also. They are broken down at the time of division and do not appear to contribute directly to the formation of the chromosomes.

There appears to be a growing tendency toward the separation of the several types of Endamoebae into subgroups. Morris (1936) suggested that the genus Endamoeba be divided into three subgenera. One of these, sub-genus Endamoeba of which the type is *blattae*, is suggested for the cockroach and termite amoebae. Two other subgenera, Placoidia with type *E. (P.) minchini* and Poneramoeba with type *E. (P.) histolytica* were used for the other types of amoebae occurring in the genus Endamoeba. The writer agrees with Morris in feeling that some sort of a separation is necessary. However, in spite of the ruling of the International Commission on Zoological Nomenclature (Opinion 99) that Endamoeba and Entamoeba are synonyms, the writer feels that it would be more logical to retain the names Endamoeba and Entamoeba, and limit the former to the cockroach and termite amoebae, and other forms that present the same characteristics of a thick-walled nucleus with a number of prominent endosomes and nuclear division lacking a metaphase plate stage. Under the latter the two subgenera suggested by Morris, Placoidia and Poneramoeba, could be used. This opinion is based on the fact that in general characteristics and in the activities of the nucleus during interphase and division, there is a more fundamental difference between the Endamoeba type and the other two than is consistent with a subgeneric

grouping. In view of the fact that later evidence has appeared, which shows quite clearly the difference between the types of amoebae, and since it seems undesirable to alter the name of the human parasites which have the great mass of literature concerning them, this division seems convenient and helpful. Dobell (1919) and Kudo (1931, 1939) have advanced this suggestion. Kudo (1939, p. 312) expresses this point of view very aptly, saying, "The generic differentiation is based upon morphological characteristics of the nucleus. Summary No. 99 of 'Opinions Rendered' by the International Commission of Zoological Nomenclature (1928) holds that *Entamoeba* is a synonym of *Endamoeba*; in the present work, however, *Endamoeba* and *Entamoeba* are separated, since the two groups of species placed under them possesses different nuclear characteristics and since it is not advisable to establish another generic name in place of *Entamoeba* which has been so frequently and widely used throughout the world."

XI. EFFECTS OF FIXATION ON THE NUCLEAR ELEMENTS

WHEN A NUCLEUS is exposed to reagents which precipitate the substances which compose it in a form sufficiently insoluble so that technical procedures, such as sectioning and staining, can be performed, it goes without saying that many profound changes of a chemical and physical nature have ensued. A comparison of the living nucleus with the fixed and stained nucleus in permanent mounts emphasizes the importance of these reactions. In the case of *E. blattae* it appears that the changes accompanying fixation and staining are more complicated and numerous than is the case with many other types of nuclei. To make them more difficult to understand, they vary significantly with different fixatives. Generally speaking, the effects involve the solution and total degeneration of the peripheral spherules, and a great increase in the visibility of the peripheral granules, the endosomes, and the central ground-plasm. Other differences of a more detailed nature are noticed when a close comparison is carried out.

The utility of any fixed and stained preparation is in proportion to the adequacy with which one can interpret the results in terms of the living nucleus. Until the question of artifact formation is understood no thorough interpretation is possible. Change of visibility in the nuclear elements is helpful, for it makes a more complete view possible, if it is certain that the final image is not too aberrant. Indeed, were it not for the changes in visibility there would be no need nor use for permanent preparations. It seems probable that any structure which appears after

fixation with several different fixatives, which shows a constancy in its position, and which is consistent in its staining reactions actually exists in the living nucleus, either as a distinct structural unit or as a region of differentiated protoplasm. Before these structures, visible only in fixed nuclei, can be interpreted in terms of their function, however, it is necessary to know their exact relation to the structures found in the living nuclei.

In order to bridge the gap between the living nucleus and the nucleus as seen in the fixed and stained mounts a series of observations were made on the process of fixation and the effects of dehydration and staining. Every fixative used for important and extensive observations and all the reagents which composed those fixatives were studied in the same way. The living amoebae were compressed slightly beneath a cover slip and studied under oil immersion before, during, and after the application of the fixing reagent. In order to facilitate a comparison with permanent mounts the nucleus was stained, after appropriate washing, with acetocarmine or methyl green. In all cases observation of the nuclei, from the beginning of the experiment until its conclusion, was continuous. The results of this preliminary study were followed by a careful comparison of the immediate effects of fixation with those occasioned by dehydration and staining. Knowing what the effects of the fixative were, the differences between the nuclei immediately after fixation and those in permanent mounts represented the effects of the later technical processes. With the hope of gaining some information as to the relative solubility, and through this, of the probable nature of the various precipitated elements, two types of permanent mounts were made with each fixative. One set of sections and smears was stained with a minimum amount of contact with water. Another set was washed for long periods of time in running water. The differences observed represented solution of precipitated nuclear elements in water, and an idea of the relative solubility of the various nuclear structures after treatment of the fixing reagent was obtained.

A. SIMPLE, UNCOMBINED FIXATIVES

Ethyl alcohol.—It is generally observed in most discussions of technique that different dilutions of alcohol cause different effects during fixation. Low grades of alcohol are said to cause much more serious malformation of the cell during fixation than absolute alcohol. In order to observe these differences, absolute alcohol, 70 per cent alcohol, and 30 per cent alcohol were used. The absolute alcohol was used at room temperature and warmed to 45-50° C. The lower grades were used only at room temperature.

The effects of alcohol as a fixative have been studied by several previous investigators. Baker (1933) describes a great deal of shrinkage, both nuclear and cytoplasmic. He also reports a tendency toward the pushing of cell and nuclear contents to one side of the cell. This was especially marked in the peripheral parts of the tissue. Strangeways and Canti (1927) report that there is no very great disturbance of cell morphology during fixation. It is interesting to note here that Baker's study was of tissue sectioned and stained after alcohol fixation, and Strangeways and Canti (1927) observed the process of fixation in isolated cells studied under dark field illumination.

With regard to the physico-chemical effects of alcohol as a fixative, there are several notes available. Fischer (1899) reports that albumins are precipitated in a form which is insoluble in water, while nucleic acids are soluble. Mann (1902) reports that nucleo-albumins and nucleins are insoluble after alcohol fixation. The precipitation of proteins, called "denaturation," is explained by Baker (1933) as one in which the protein linkages are affected, altering the solubility of the compounds and their affinity for acids and bases, without appreciably affecting their chemical nature.

In the study of the immediate effects of fixation the alcohol was applied to the edge of the cover slip and drawn under it rapidly with a piece of paper toweling applied to the opposite edge. It must be noted here that some dilution of the alcohols must have occurred during this. The small amount of water and the large amount of alcohol used indicates that the dilution was not great. Fixation with alcohol was slow, requiring from 2 to 3 minutes for the visible alterations of nuclear appearance to cease, although the animal was killed almost instantaneously. Strangeways and Canti (1927) reported that alcohol fixation was instantaneous. At the moment of fixation the nuclear membrane became thinner, probably at least partially the result of the lifting of the cover slip by the advancing wave of the fixative. No other visible change affected the nuclear membrane. No change in the position, shape or size of the peripheral granules was observed, but they became much more refractive. The peripheral ground-plasm became much darker and was precipitated in very fine granules. There was no effect on the peripheral spherules. This failure of the alcohol to dissolve the peripheral spherules during fixation seems to indicate that the belief of Janicki (1909) that the spherules were dissolved by the alcohols during dehydration is probably incorrect. The endosomes, sometimes partially hidden by the peripheral spherules, became slightly more refractive the instant that the alcohol struck the animal. After this there was no further visible change in the endosomes. The central region, transparent in life, underwent the most

striking series of alterations. A number of fine strands appeared first, several seconds after the alcohol came in contact with the amoeba. These became more prominent, and about a minute after fixation had begun a number of fine granules appeared on the strands. Several moments after the strands became prominent the central ground-plasm began to precipitate. The precipitate was in the form of extremely small particles which gradually increased in numbers and ultimately obscured the strands and granules. When fixation occurred in the proper kinetophase stage a hyaline body could be observed. When this homogeneous structure was noticed at one pole of the nucleus, it was accompanied by a number of delicate granules in the ground-plasm of the central region which appeared just before the ground-plasm was precipitated. These were not observed in interphase nuclei.

The most characteristic phenomenon observed in alcohol fixation was the gradual appearance of the various nuclear elements. In almost every other fixative tried fixation was instantaneous. In every experiment the elements formed slowly and in all cases the various nuclear elements appeared following the same temporal sequence. The addition of methyl green to the fixed nucleus showed that the peripheral granules were basophilic, the endosomes somewhat more so, and the hyaline body somewhat less so. After some time the whole nucleus became lightly stained with the green dye.

While still lying in the alcohol the nuclei were very accurately and well preserved. Shrinkage was much less than had been anticipated, especially in the lower grades of alcohol. The nuclear elements appeared to be preserved in approximately natural conditions, and there was no observed tendency of the cell or nuclear contents to draw to one side of the cell. The results of observations on the immediate effects of fixation appear to confirm Strangeways' and Canti's (1927) report that alcohol does not cause any striking alteration of form.

It was only in permanent preparations that aberrations and other indications of poor fixation were found, as will be noted below. The nuclear membrane was homogeneous and about the same regardless of the percentage of alcohol or temperature. It was acidophilic, and resisted staining with basic dyes. The membrane was greatly wrinkled in slides fixed in 70 per cent alcohol, due to shrinkage of the nucleus. In many cases the uneven shape was so disturbing that the nuclear elements within could not be studied satisfactorily. This effect was much less intense in absolute or in 30 per cent alcohol. The low grade of alcohol, insofar as nuclear shape and amount of shrinkage was concerned, was superior to 70 per cent, and very little inferior to absolute. Few nuclei were misshapen, and, based on comparative measurements, seemed to

show but little shrinkage. There was no indication that the substance composing the membrane was poorly preserved. The peripheral ground-plasm was precipitated as a homogeneous or very finely granular region, distinct from the central ground-plasm. Again the comparative shrinkage effects could be noted by comparing the amount of separation of peripheral and central ground-plasms. With fixation in hot absolute, the amount of shrinkage was less than with cold absolute. It was very great with 70 per cent alcohol. In 30 per cent, however, the shrinkage was reduced to a minimum. The central and peripheral regions were in contact along the whole periphery (cf. Figs. 44, 45). The substance of the peripheral ground-plasm was in finer particles in the slides fixed with 30 per cent than with absolute alcohol. The peripheral ground-plasm was acidophilic but did not resist staining with basic dyes. The peripheral granules were found in a comparatively natural condition in nuclei fixed with absolute alcohol, and exposed to little contact with water, but were dissolved away or rendered much less conspicuous by washing (cf. Figs. 44 and 45). Reduction of the percentage of alcohol reduced the resistance of the granules to solution, so that after fixation in 30 per cent alcohol they were usually dissolved or modified even when contact with water was slight. The peripheral spherules were found after fixation in all grades of alcohol. They were usually regular in shape, but occasionally irregularities in outline and signs of fusion were observed (Fig. 47). The irregularities were never great, and were not increased by exposure to water. In many fixed nuclei the spherules were clumped near one pole and filled the whole peripheral region at that point (Fig. 43). During kinetophase they were found between the two poles, and often showed a tendency to form irregular rows at that stage (Fig. 47). It was interesting to observe that fixation in 30 per cent alcohol made the spherules more resistant to washing than fixation in absolute. This was thought at first to indicate solution of the spherule substance in alcohol, but after several days in absolute alcohol, no modifications beyond that of normal fixation were observed. In all cases the spherules were resistant to a high degree to staining with acid and basic dyes. In rare cases—and these usually near a division—the spherules were tinted very lightly by orange G and light green. They were never tinted by eosin. The endosomes were precipitated by all grades of alcohol, but the higher grades gave a more perfect picture of them. They were invariably stained with basic dyes, but never with the Feulgen reaction. After washing they were sometimes partially fused together (Figs. 45, 46) and always showed clear evidences of ragged and tattered edges. This effect was much more clearly indicated in elongated than in spherical endosomes. Lying between the chromosomes at the poles were the endosomal spherules in

dividing nuclei. These were usually invisible in nuclei fixed in low grades of alcohol, and very imperfectly preserved in higher grades (Fig. 47). There was no difference in their resistance to washing and their general staining reactions between hot and cold absolute fixation. The central region appeared as a reticulum or as a homogeneous region (Figs. 44, 45). In unwashed nuclei a very irregular and indistinct region at one pole of the central region was occasionally found. It had a higher affinity for basic dyes than the remainder of the central region, and it is thought that it represented a remnant of the hyaline body. It was never observed in washed nuclei. The ground-plasm itself showed no particular differences between fixation in low and high grades of alcohol, except that the particles appeared to be slightly smaller in nuclei fixed in hot absolute and 30 per cent alcohols. Shrinkage of the central ground-plasm appeared to parallel that of the peripheral ground-plasm, being lowest in hot absolute and 30 per cent alcohol. The ground-plasm was almost neutral in staining reactions, showing affinities for neither acidic nor basic dyes, nor resistance to staining with them. On occasions the central region was eccentric, suggesting the condition mentioned by Baker (1933). In nuclei in early kinetophase, strands appeared which seem to be identical with the chromosomal strands observed in compound fixatives (see below). In middle kinetophase, the chromosomes were found clumped together at the poles (Figs. 47, 48). In all cases they were greatly fused together, with indistinct outlines, showing clearly that they had been partially dissolved. This was most clearly observed in nuclei which had undergone prolonged washing. Lower grades of alcohol preserved the chromosomal substance less perfectly than higher grades. The chromosomes showed little affinity for basic dyes, and were but very slightly colored by the Feulgen reaction, or, more frequently, and always in the washed preparations, were completely negative to the Feulgen test. The chromosomal substance was colored rather deeply by light green and orange G.

After prolonged washing nuclei fixed with alcohol were sometimes entirely empty of all the nuclear elements. Only the nuclear membrane, sometimes retaining its spherical shape, and at other times greatly wrinkled and misshapen, remained. This occurred after all grades of alcohol, and, it may be noted here, after all other fixatives. It appears that this is due either to some abnormal condition of the nucleus itself or to uneven fixation. The fact that it occurred in all fixatives suggests that probably some abnormal condition of the nucleus itself occasioned the solution of all of the inner elements.

The results of alcohol fixation may be summarized in the following terms. Nuclear shrinkage is greatest in the medium grade of alcohol. The substance of the nuclear membrane is well preserved and resistant

to washing. The substance of the peripheral ground-plasm is most satisfactorily preserved in high and low grades and is resistant to washing. The peripheral spherules are well preserved and resistant to washing. The peripheral granules are imperfectly preserved, best by the highest grades, and are more or less soluble in water. The endosomal substance is imperfectly preserved, especially in lower grades, and especially in nuclei which are dividing or are in the early interphase stages. It is less soluble than the substance composing the peripheral granules, but shows distinct signs of dissolving, even in nuclei fixed in hot absolute alcohol. The central ground-plasm is preserved rather well in interphase nuclei, and is not dissolved during after-treatments. The chromosomes are very imperfectly preserved, especially in the lower grades of alcohol, and are clumped and partially dissolved during after-treatments even when fixed in absolute alcohol and exposed as little as possible to water. They are but slightly positive or wholly negative to the Feulgen nucleal test. The hyaline body, although well preserved in nuclei still lying in the fixative, is extremely soluble, and usually disappears almost entirely even when the contact with water is reduced to a minimum. On the whole, fixation appears to be very good while the nucleus still lies in the fixative, but during after-treatments aberrations of various kinds occur, which frequently produce extremely imperfect and unnatural images. Surprisingly enough the best fixation was obtained with the highest and lowest grades of alcohol, and the poorest by the medium grade. No explanation of this has been adduced.

Dioxane.—The use of dioxane for cytological technique is so recent that little is known of its effects on tissues and cells. It has replaced alcohol for dehydration to no small extent, especially before imbedding in paraffin, and since it was used for dehydration during part of this study, its effects on the nucleus were studied in order to determine if it was likely to affect the solubility of compounds precipitated by other fixatives.

The writer is not aware of any information concerning the chemical compounds precipitated by dioxane, nor their solubility after such precipitation. It is recommended by some cytologists to replace alcohol in certain of the alcoholic fixatives, and new formulae using dioxane as a fixative have been devised (see McClung, 1938).

In observations of the immediate effects of fixation, the death of the organism was instantaneous, and the nuclear changes also were instantaneous, resembling other fixatives more than alcohol in this particular. Cytoplasmic shrinkage was very small, but nuclear shrinkage was quite noticeable, and was estimated at about 20 per cent. The nucleus was drawn out of shape in many cases, usually becoming oval or indented

during the shrinking process. The nuclear membrane was poorly preserved. It was noticeably thinner, and in many cases the material composing the membrane ran into the cytoplasm in the form of irregular, short filaments of clear, hyaline material (Fig. 36). A profound alteration of the peripheral zone accompanied fixation. The ground-plasm was no longer distinctly differentiated from the spherules and granules. The spherules were partially dissolved and ran together confusedly, resulting in a very characteristic appearance. This may have resulted partially from a loss in distinctness of outline resulting from a change in refractivity, and results obtained in permanent preparations seemed to indicate that this was the case. The peripheral granules were apparently precipitated, but were little, if any, more prominent than in the living nuclei, and the indistinct nature of the background made it extremely difficult to observe them. The endosomes were distinct, regular in outline, and appeared to be well preserved. They were much more prominent in fixed than in the living nuclei. The central region contained a coarse precipitate in which neither hyaline body nor centriole was ever observed.

In permanent preparations the nucleus was deformed and had undergone a great deal of shrinkage. The homogeneous nuclear membrane showed a slight affinity for basic dyes, especially for haematoxylin. The peripheral spherules were present in large numbers in almost all nuclei, although in a few, rare cases they had been completely dissolved. Except for these exceptional nuclei, they appeared to be well preserved. They were resistant to staining with dyes, but occasionally were very lightly tinted by light green or orange G. The spherules were found in the median part of elongated dividing nuclei, where they were arranged in irregular rows and could be distinguished from the endosomal spherules by their staining reactions. The peripheral granules were present in nuclei which were exposed to very little water, but dissolved out very readily. Two hours of washing was sufficient to completely dissolve the peripheral granules. When present, they were basophilic. The endosomes were poorly preserved, usually being quite misshapen. They were distinctly less basophilic after washing, and in washed nuclei showed evidences of fusion and partial solution. In dividing nuclei the endosomal spherules were quite indistinct and frequently had lost their affinity for basic dyes to a considerable extent. Like the endosomes, they were often partially fused. The central region was not drawn away from the peripheral region, indicating very little shrinkage. It was somewhat more basophilic than the peripheral ground-plasm in unwashed nuclei, but this distinction was lost in washed nuclei. In unwashed nuclei the central ground-plasm showed a light, diffusely positive reaction to the Feulgen reagents during early and late kinetophase stages. In no case

was a hyaline body or centriole observed. Chromosomes were never found, although in several dividing nuclei a homogeneous region of differentiated material which, from its position, was apparently derived from the chromosomes was found. In unwashed material this region was somewhat more basophilic than the surrounding material.

The effects of dioxane may be summarized as follows. The process of fixation entails a considerable nuclear shrinkage, and appears to involve a poor preservation of the substance of the nuclear membrane. The apparent partial solution of the peripheral spherules is not observed in nuclei in permanent preparations, so it appears that this, and other observations of nuclei lying in the fixative, are partially determined by alterations in the refractive index resulting from the dioxane. The endosomes are apparently well preserved in nuclei still lying in the fixative, but show signs of solubility by fusion and loss of basophilic material in permanent preparations. The central ground-plasm is well preserved, insofar as shrinkage is concerned, but the basophilic elements are lost during extended periods of washing. The chromosomes are very poorly preserved, and the hyaline body and centriole seem to be completely lost, even in unwashed nuclei. Comparing this with the results obtained with alcohol, it is evident that the two reagents cannot be considered as identical in their effects. Neither reagent is sufficient, alone, to give good fixation, but they fail for different reasons. It is worthy of note that of all the reagents tried, dioxane was the only one to fix the nuclear membrane poorly, and there is some evidence that the substance of the nuclear membrane is soluble in dioxane.

Acetic acid.—Acetic acid is widely used as a nuclear fixative. It is not considered a satisfactory fixative alone, for it does not fix the cytoplasm and its effect on the chromatin is too violent. Baker (1933, p. 36) states, "Acetic acid is an excellent fixative for showing up nuclei clearly for histological work, but for a cytological study of the interphase nucleus it is useless. Chromosomes, however, it preserves excellently, and acetic acid is a component of all fixatives for chromosome studies. . . . Nevertheless it is not proper to use acetic acid (except perhaps very dilute) in studying the condensation of the chromatin to form chromosomes, nor the telophase transformation of the chromosomes into the interkinetic nucleus." Very little information is available concerning the chemistry involved in acetic fixation. Baker explains that its swelling action depends on the absorption of water because of an increase in the osmotic pressure in the fixed cell. The osmotic change is the result of the formation of a salt of the protein and the anion, which dissociates as a non-diffusible protein cation and an acetate anion, which is held to the cation by electrostatic attraction. The precipitate formed by acetic acid and albumin is

soluble in an excess of acetic acid. Nucleic acids, nucleoproteins, and nucleins are precipitated, the first two, at least, being insoluble in water. Acetic acid was used as a fixative at room temperature and warmed to 45-50° C. in this study. Glacial acetic, 10 per cent acetic, and 5 per cent acetic were used at both temperatures. Only room temperature was tried for solutions of 2 per cent, 1 per cent, and 0.5 per cent acetic.

Death was instantaneous with the acetic acid solutions used. A coarse precipitate of the cytoplasm formed immediately in all cases except fixation with 1 per cent and 0.5 per cent acetic. In these last mentioned dilutions the cytoplasm did not appear to be precipitated, and would disintegrate shortly after fixation, usually floating away and carrying the nucleus with it. For this reason, the observations of the nuclear effects with 1 per cent and 0.5 per cent acetic are less complete than in the case of the more concentrated solutions. Nuclear and cytoplasmic swelling occurred with fixation. The nuclear swelling was greater than the cytoplasmic swelling, reaching a maximum of about 76 per cent with glacial acetic. Even the lowest grades of acetic caused some swelling.

As a result of fixation, the nuclear membrane became much thinner. This appeared to be at least partially the result of the great swelling of the nucleus. It was homogeneous and somewhat less refractive than in life. The peripheral ground-plasm was precipitated as a finely granular region, with a number of prominent peripheral granules imbedded in it. The spherules were dissolved rapidly in the lower grades of acetic acid, but in the higher grades dissolved very slowly, or not at all. The endosomes were usually more prominent than in the living nucleus after fixation, except in the case of glacial acetic, when they were very little more refractive than in life. Usually homogeneous, the endosomes occasionally showed evidences of vacuolation. The central region was partially obscured by fixation, but appeared to be precipitated in very fine particles. Neither centriole nor hyaline body was ever observed in it. Acetocarmine and methyl green stained the peripheral granules and the endosomes, but not very selectively. All of the nucleus would gradually become stained, and frequently the cytoplasm, too, would stain with the basic dye. The first to stain, however, were the peripheral granules and endosomes. No evidence of a distinct basophilic nature could be detected in the central region.

In permanent preparations the nuclear membrane was homogeneous, staining quite deeply with the acid dye. After fixation in hot acetic acid, it showed a slightly higher affinity for basic dyes than in the other cases. In the lower grades of acetic, the nuclear membrane appeared to be thinner than in the higher grades (cf. Figs. 49, 53). Nuclei fixed in grades lower than 5 per cent frequently appeared greatly wrinkled, ap-

parently a result of incomplete fixation of the material within the nucleus as well as of the nuclear membrane.

The appearance of the peripheral region depended to a great extent on the grade of acetic acid used. The ground-plasm was homogeneous in nuclei fixed in glacial acetic acid, sometimes indistinguishable from the central ground-plasm, and sometimes clearly separate (cf. Figs. 51 and 53). With increased contact with water the differentiation of the central and peripheral ground-plasms decreased, but this may have been partially an effect of the destruction of the endosomes and the peripheral granules during washing. In 10 per cent acetic the peripheral ground-plasm was usually an irregular reticulum. In 5 per cent acetic, the peripheral ground-plasm was more or less dispersed if fixation was carried out at 45° C. At room temperature with 5 per cent acetic and all of the lower grades, there was no peripheral ground-plasm, as such, in the nucleus. All of the nuclear contents were clumped together in the center or at one side of the nucleus. This clumping of substances was probably at least partially caused by the absence of a supporting peripheral ground-plasm. It seems, from the differences between fixation of the peripheral ground-plasm in hot and cool 5 per cent acetic acid that the precipitation of the peripheral ground-plasm in the hot 5 per cent acetic was due to the heat and not the action of the acetic. The peripheral spherules were partially destroyed in hot glacial acetic acid (Fig. 51), and were increasingly dissolved as the percentage of acetic acid was reduced. They were more satisfactorily preserved in nuclei fixed with hot acetic than cold acetic. Even with the warmed fixative, they were completely destroyed in nuclei fixed with lower grades of acetic. The peripheral granules were most prominent in nuclei fixed with 10 per cent acetic (Fig. 49). In higher and lower grades they were rarely found, except in occasional nuclei in the unwashed preparations (Fig. 53). In washed slides in all percentages of acetic acid, used either hot or cold, the granules were dissolved (Fig. 52).

The endosomes were poorly preserved by acetic acid in most cases. With glacial acetic fixation they are quite basophilic, but tend to fuse together, especially after washing (Figs. 52, 53). When the endosomes have not fused together the differentiation of a darkly-staining cortex and lightly-staining core is commonly observed (Fig. 51). Not uncommonly the endosomes are completely dissolved in preparations washed for prolonged periods. Insofar as the endosomes were concerned fixation in 10 per cent acetic was like the glacial acetic fixation. The results of cold 10 per cent acetic fixation were similar to those observed in hot 5 per cent, and in cold 5 per cent acetic and all lower grades, the endosomes were quite soluble. The tendency toward fusion of the

endosomes in nuclei fixed in 10 per cent acetic acid was less marked than in nuclei fixed with glacial acetic, especially when the nuclei were in the early interphase condition. Hot fixation usually favored endosomal fusion. The observations of endosomal spherules closely paralleled those on the endosomes, whenever they were observed. In the glacial acetic preparations no dividing nuclei were found, so that the observations are incomplete. Similarly none were found in the lowest grades, and all observations are on dividing nuclei which were encountered in slides fixed in either 10 per cent or 5 per cent acetic.

The central region appeared to be homogeneous after fixation in glacial acetic, and usually merged with the peripheral zone. In some cases the central region was more basophilic than the peripheral zone (Fig. 51), and in early or late kinetophase a diffusely positive Feulgen reaction was observed, even in washed nuclei. Although the central region was homogeneous after fixation in hot 10 per cent acetic, the cold 10 per cent fixation gave it a granular appearance (Fig. 49). With hot 5 per cent acetic the central region was fibrillar and granular, and several nuclei in which remnants of a hyaline body could be seen were found. Fixation in cold 5 per cent, or in lower grades was so incomplete that no observations could be made successfully. So much of the nuclear substance was dissolved that identification of particular elements was uncertain. In several nuclei fixed with glacial acetic, remnants of the centriole were found, and one nucleus seemed to contain a dividing centriole (Fig. 53). Chromosomes were well preserved by acetic acid, especially in 10 per cent. Their contours were regular, and appeared quite precise. The staining reaction with Feulgen appeared to be positive, although so few dividing nuclei were present in the Feulgen material that a definite statement cannot be made. With haematoxylin, the chromosomes showed a slight affinity for the basic dye.

Summarizing the results of the observations on acetic acid fixation, the following conclusions may be drawn. Acetic fixation involves a considerable swelling of the nucleus and an accompanying attenuation of the nuclear membrane. The substance of the membrane is usually well preserved, except in low grades of acetic. The peripheral ground-plasm is precipitated in an insoluble form by the high grades of acetic, but in the lower grades the solubility of the substances precipitated increases. Peripheral granules are never well preserved, but are found most satisfactorily preserved in the highest grades of acetic only. The peripheral granules are preserved most satisfactorily by 10 per cent acetic acid, and with an increase or decrease are usually absent, or are less basophilic. Endosomes are poorly preserved by acetic acid, usually fusing together, or dissolving completely during staining procedures. Immediately after

fixation, however, before exposed to water for any length of time, they appear to be comparatively well preserved. The central region contains a centriole in some nuclei, although this is not invariably true. The hyaline body is not preserved. The ground-plasm is precipitated with little shrinkage in high grades of acetic, but as the percentage of acetic acid decreases, the fixation is progressively poorer, the precipitate formed becoming more soluble in water. Chromosomes are well preserved, especially in 10 per cent acetic, and a positive reaction with the Feulgen test is suggested.

Mercuric chloride.—A saturated solution (about 6.5 to 7 per cent) of mercuric chloride was used for fixation at room temperature and at 45-50° C. A 3 per cent solution was also employed at room temperature. The detailed effects of fixation were somewhat different in the three procedures. In the study of the immediate effects of fixation, a saturated solution was used.

The action of mercuric chloride during fixation is not very completely understood. Mann (1902, p. 77), writes, "With ammonia it [mercuric chloride] forms the mercuriammonium chloride or infusible white precipitate HgCl_2 plus $2 \text{NH}_3 = \text{NHgH}_2\text{Cl}$ plus NH_4Cl . Analogously to this equation it probably combines with the nitrogenous constituents of the cell." This long-accepted view of sublimate action was denied by the work of Thomas and Norris (1925) who found that the coagulation of albumin produced by ferric chloride in dilute solutions was soluble in an excess of ferric chloride, but that a new precipitate appeared in more concentrated solutions. Baker (1933) believes that sublimate acts in the same way as ferric chloride. The precipitate formed in dilute solutions is a compound, a mercury or ferric albuminate, during the formation of which the albumin is acting as an anion because the salt is on the basic side of the isoelectric point. But as the concentration is increased the pH of the fluid gradually goes toward the acid side due to the ionization of the mercuric chloride to hydrogen and chloride ions plus $(\text{HgCl})_2\text{O}$ or HgClOH . Mann's statement that it ionizes to HgOH and 2HCl was disproved by Luther (1904). As the concentration of the fixative is increased a precipitate of denatured albumin forms for entirely different reasons than the first. This denatured protein, different from the denatured protein resulting from precipitation by alcohol, carries a varying amount of the mercury salt with it. No union between these occurs, however, for all the mercury can be washed out. Thomas and Norris consider that this precipitation with ferric chloride is identical with heat coagulation. This view depends on the fact that salts are invariably necessary for heat coagulation and that salts of heavy metals are the only ones which will cause precipitation of proteins at room temperatures.

It is worthy of note that the heat coagulations of albumins in general has been known to require hydrogen ions for a long while. Mann (1902, p. 67) says, "Any factor which tends to prevent the formation of hydrogen ions will also prevent coagulations." Any salt of a heavy metal favors the liberation of hydrogen ions. This may be an important factor in producing the coagulation resulting from mercuric chloride solutions.

Fischer (1899, p. 23) reports, "Wie diese [Peptone, Deuteralbumose, and Protalbumose], werden auch Albumin, Globulin, Casein, und Conglutin, Hämoglobin, Nuclein und Nucleinsäure als alkalischer und säurer Lösung unlöslich ausgefällt."

Not much of importance has been found concerning the desirability of mercuric chloride as a fixative. Strangeways and Canti (1927) report that a coarse precipitate is formed in nucleus and cytoplasm by this salt. Baker (1933) accuses it of causing a very unlikelike fixation, and says that the good stainability of material after sublimate fixation is its chief advantage.

Death in mercuric chloride is instantaneous, although several moments are required for fixation to go to completion. Cytoplasmic shrinkage is considerable, but nuclear shrinkage is small. The nuclear membrane was homogeneous after fixation, but a distinct loss in refractivity was observed. In the peripheral zone the ground-plasm was precipitated in small particles. The whole of the ground-plasm appeared to be homogeneous after fixation. Peripheral granules were not visibly altered during fixation, and did not increase in refractivity or numbers. The peripheral spherules were not visibly altered when the sublimate first came in contact with the nucleus, but in about a minute they became noticeably smaller, and were usually completely dissolved in about two minutes. No visible changes other than a gradual decrease in size accompanied their solution. The endosomes appear to be homogeneous after fixation, and much more refractive than in life. The central region was almost homogeneous after fixation in some nuclei, and was finely granular in other nuclei. In a few cases a central granule could be observed in the center of the central region. In nuclei in the correct stages a hyaline body could be observed. It was indistinguishable from the endosomes insofar as shape or refractivity were concerned, but occupied its characteristic position, and was stained much more lightly with methyl green than the endosomes.

In permanent preparations the nuclear membrane was homogeneous and distinctly acidophilic. It was consistently thinner than in permanent preparations fixed with compound fixatives, but there was no indication of solution of the substance composing it even after prolonged washing.

The peripheral ground-plasm was a homogeneous region, composed of

fine granules. It was acidophilic, although in a few nuclei it was tinted lightly by the basic dye, especially in nuclei fixed with the cold saturated solution. The peripheral spherules were excellently fixed by the hot saturated mercuric chloride, almost filling the whole peripheral region, and obscuring any peripheral granules which might have been present. Peripheral spherules were but very occasionally found in nuclei fixed in the cold saturated, and never in the 3 per cent, solutions. Hot and cold saturated solutions caused a slight separation of the central and peripheral regions, but this effect was little noticed in nuclei fixed with 3 per cent sublimate. Peripheral granules were occasionally found in the nuclei fixed with a cold saturated solution, but were much less prominent in material fixed in a 3 per cent solution.

The endosomes were essentially the same in all of the sublimate-fixed nuclei. They were distinctly basophilic, but remained uncolored by the Feulgen reaction. The larger spherical endosomes were quite frequently vacuolated, but the elongated endosomes never showed this structure. The endosomes were always sharply outlined, and the substance, except for the vacuolated ones, was homogeneous throughout.

The central region was finely granular and reticular in saturated solutions, and homogeneous in 3 per cent solution. In nuclei fixed in 3 per cent sublimate, the differentiation of the peripheral and central ground-plasms was very difficult, for they were not drawn away from each other, and both were homogeneous and acidophilic to very slightly basophilic. After fixation in cold sublimate only was a hyaline body observed. It was most prominent in Feulgen-light green preparations, where it was distinguished by its affinity for light green and its clear hyaline appearance.

Two interesting points appear in the results of mercuric chloride fixation. The first is the differences observed in the size of the particles of the precipitated ground-plasm after treatment with dilute and saturated solutions of sublimate. The fine particles produced during fixation with the 3 per cent solutions cause a homogeneous appearance which contrasts very strongly with the finely granular appearance resulting from fixation with saturated solutions. When albumin is precipitated in test-tube experiments, active precipitants have a tendency to form flocculent precipitates, while less active ones show a light opalescent coloration. These opalescent colors in the test-tube experiments appear to be comparable to the homogeneous appearance resulting from fixation in the dilute solution. The coarser precipitate forms as a result of stronger concentrations in both nucleus and cytoplasm. If the coagulation of albumins by mercuric chloride is comparable to heat coagulation, an increased effect should be apparent in the heated solutions. No such sum-

mation effect was found, except for the preservation of the peripheral spherules, which were preserved only in the heated solution. In other simple fixatives the heated solutions frequently showed a more accurate and complete preservation of the peripheral spherules whether the cold fixative did or did not preserve them, which seems to indicate that the peripheral spherules are preserved by heat. The peripheral spherules, however, are soluble in cold mercuric chloride, as was observed in studies of the immediate effects of fixation. A greater amount of detailed work is necessary before any conclusions can be drawn, but the inference seems clear that, regardless of the way that albumins are precipitated by mercuric chloride, the mercuric chloride fixation of the spherules does not resemble heat coagulation. It appears that in the case of many fixatives their total effect is very incompletely known, and they may react very differently with different elements.

Another interesting observation was made on mercuric chloride fixation. The nuclei were extremely lifelike in appearance, particularly after fixation in a hot saturated solution. This appears to be different than is the case with most other types of nuclei, which are said to be abominably fixed by sublimate. In the case of *E. blattae*, the nucleus is extremely lifelike, marred only by the very finely granular appearance of the peripheral ground-plasm, and the slight increase in refractivity of the central ground-plasm. Even shrinkage is extremely small.

Formaldehyde.—Undiluted formalin (40 per cent formaldehyde) was used for fixation at room temperature and at 45-50° C. A 10 per cent solution of formalin (4 per cent formaldehyde) was used at room temperature.

Most of the observations on fixation processes were made with undiluted formalin. A few trials with the 10 per cent solution were undertaken, but the results of the first few coincided with the observations made with formalin, and no great number were attempted. Not enough work was done with the 10 per cent solution to draw any valid conclusions.

Cytoplasmic shrinkage was very small, and the nuclear shrinkage was so slight that none could be measured. Death was instantaneous and all of the visible changes accompanying fixation were completed in one minute. At the moment of fixation the nuclear membrane appeared to become somewhat thinner. The substance of the membrane remained homogeneous, and no alteration of refractivity was observed. The peripheral zone underwent very little visible alteration during fixation. The peripheral ground-plasm remained homogeneous, and no precipitate was formed. The peripheral spherules became slightly smaller, and appeared to be a little less refractive, but no other changes could be observed. The peripheral granules were no more distinct after fixation than before

fixation. The endosomes gradually became more prominent, until about a minute after the fixative was applied. They appeared to be homogeneous, and vacuolation was not observed. The central region remained hyaline after fixation. No visible precipitation occurred, and the central ground-plasm remained invisible.

In permanent preparations the nuclear membrane appeared to be homogeneous and acidophilic. It was usually most deeply stained with light green. In some cases where shrinkage had occurred during dehydration the membrane was greatly wrinkled. This was most noticeable in sectioned amoebae which had been subjected to prolonged periods of washing in running water. In unwashed preparations this was very rarely noticed. There were no obvious visible differences in the fixation with undiluted and 10 per cent formalin.

The peripheral zone was very characteristic in appearance after formalin fixation. The ground-plasm was homogeneous and showed some affinity for both acid and basic dyes. It was difficult to observe because of the large numbers of peripheral spherules which were invariably present (Fig. 54). Hot and cold fixatives appeared to preserve the spherules equally well, and they showed no tendency to dissolve after fixation in the 10 per cent solution. They were invariably resistant to staining with both acid and basic dyes, but were occasionally very lightly tinted with the acid dyes. No evidences of fusion or partial disintegration were ever observed. The peripheral spherules were present in such large numbers that they usually obscured the peripheral granules, just as they do in living nuclei. In some cases a few granules, rather basophilic, could be found.

In all preparations the endosomes were homogeneous unless very large, when vacuoles were occasionally observed. They were stained with basic dyes, but were also deeply colored by acid dyes in wholly destained preparations and in Feulgen-light green preparations. They were not colored by the Feulgen reaction. The basic dyes appeared to stain the endosomes less deeply than after some of the other fixatives. Occasionally a dark basophilic granule was observed in the center of larger, non-vacuolated endosomes. No alteration of the endosomes resulted from prolonged washing.

The central region was homogeneous, and indistinguishable from the peripheral ground-plasm. In no case were the central and peripheral ground-plasms separated by fixation shrinkage, either in washed or unwashed preparations (Fig. 54). In most nuclei the central ground-plasm was stained very lightly with the acid dye, or occasionally, very lightly with the basic dye. Centriole chromosomal strands and hyaline bodies were sought in vain. During division the central region changes

could not be studied, and the chromosomes were not distinct (Fig. 55), but formed a homogeneous region at the pole of the dividing nuclei, slightly tinted with purple in Feulgen preparations. These nuclei were almost identical in appearance with the descriptions given by Kudo (1926) of living nuclei during division, except that the clump of material at the pole of the nuclei which was not invaded by the peripheral granules and spherules was tinted with the basic dye or with the Feulgen reaction.

It was interesting to observe that nuclei parasitized by *Nucleophaga*, described by Mercier (1907, 1910) and Kirby (1927), appeared in nuclei fixed with formalin in an extremely lifelike condition (Fig. 56). These nuclei were characterized by the lack, or reduced amount, of endosomal substance, and the presence of the large spherical parasites.

As can be seen from the above description, the action of formaldehyde leaves the nucleus in a most lifelike condition, insofar as appearance is concerned. This is especially unexpected when one considers the large number of chemical reactions which supposedly accompany fixation with formalin (see Mann, 1902). Fixation of most of the substances entails the formation of additive compounds with formaldehyde, with the release of water. The structures are apparently coagulated without causing any great alteration of the physical state of the nucleus, resulting in a very slight alteration of the refractivity of the parts. This is not a new observation, for Noël and Mangelot (1922), after using formaldehyde on a large number of different kinds of plant and animal nuclei, came to the conclusion that formalin, diluted, is an excellent fixative. Baker (1933, p. 32), remarks, "Noël and Mangelot (1922) claim that the use of formaldehyde gives a very lifelike fixation of the nucleus, unlike standard fixatives. For some reason it is an atrocious fixative for the mammalian testis. Shrinkage is so great that sections are scarcely recognizable." Fixation of *E. blattae* appears to resemble that reported by Noël and Mangelot, especially for organisms fixed by the smear technique. In sectioned preparations, especially if any prolonged period of washing is allowed, considerable shrinkage occurs.

Indeed, formalin fixation is so lifelike that it is hardly more advantageous for study than the living nucleus, except for the clearer image of the endosomes made possible by staining, and the permanence of the preparations. In only one respect does *E. blattae* differ from the material studied by Noël and Mangelot. They report that chromosomes are excellently preserved, while in *E. blattae* they are not distinct.

Chromic acid.—The study of chromic acid fixation was made with a one per cent solution, used at room temperature and at 45-50° C. for permanent slides, and at room temperature for the observation of the immediate effects of fixation.

Death was instantaneous in chromic acid, but the visible alteration of the nuclear elements was not complete for several minutes. Cytoplasmic and nuclear shrinkage was very slight. The nuclear membrane became somewhat thinner at the moment of fixation, but remained homogeneous and highly refractive. The peripheral ground-plasm was precipitated in fine granules which clumped together in indefinite aggregations and usually obscured the peripheral granules to some extent. The granules, insofar as they could be observed, underwent no visible changes, and were not more refractive after fixation. At the moment of fixation the peripheral spherules became darker and noticeably less refractive. In a few moments they began to dissolve, and gradually disappeared. There was no evidence of fusion of the spherules while they dissolved. The endosomes were well preserved. They were distinctly outlined, and were composed of two types of substances which were visibly differentiated. The outer layer of the endosomes was more dense and refractive. The inner portion was composed of material apparently less dense and less refractive. The larger endosomes showed a vacuolated structure with the less refractive material collected in the vacuoles. The central ground-plasm was precipitated in fine particles which tended to aggregate into clumps similar to those observed in the peripheral ground-plasm. The hyaline body and centriole were never observed.

In permanent mounts made with material fixed in chromic acid, the nuclear membrane retained its homogeneous and refractive nature. The membrane was invariably acidophilic, although in a few cases some affinity for the basic dyes was also noticed. The peripheral ground-plasm was precipitated as a coarsely granular region which usually contained a combination of the acid and basic dyes (Fig. 58). Scattered throughout the peripheral region were the basophilic peripheral granules. No indications of solution of the peripheral granules were noticed in the slides washed for prolonged periods. The peripheral spherules were not found, even in slides in which contact with water had been reduced to a minimum. The endosomes usually appeared to consist of an outer, more basophilic cortex, and an inner, less basophilic core. The outer material was sharply outlined, and distinctly differentiated from the inner material. In some cases the endosomes were vacuolated. There was no evidence of solution of the material composing the endosomes in the washed slides. The endosomes were not colored by the Feulgen reaction. The central ground-plasm formed a coarse precipitate which was not visibly differentiated from the peripheral ground-plasm, and reacted similarly to it with basic and acidic dyes. Nuclei in which the chromosomal anlage were visible, however, showed a distinctive differentiation of central and peripheral regions, with a more homogeneous appearance of the central region and slightly basophilic strands scattered throughout the central

region (Fig. 57). The hyaline body was never observed. The centriole, likewise, was not visible. No dividing nuclei were found in the preparations made with chromic acid.

Although chromic acid has been used on animal substances in tanning for many years its action is not completely understood. When it strikes the cell, denaturation of the protein is thought to be the first step in fixation. A slower hardening action is also involved, according to Berg, who attributes this to the anion HCrO_4 . The fixation process seems to be accompanied by the formation of compounds of the protein with the chromic acid, but the manner of its formation is not very clearly understood. Berg (1927) believes that this compound is linked with the oxidizing powers of the acid. Baker (1933, p. 42) says, "Exactly what happens is not known, but part of the process is an oxidation, resulting in the formation of Cr_2O_3 , which gives a greenish color to the tissue. This is certainly not all that happens, for oxidizing agents are by no means necessarily fixatives." Its action may be summarized by saying that it is a precipitant for almost all proteins. It is thought by Baker to have no effect on the fat or mitochondrial substance. In view of the incomplete knowledge of the effects of chromic fixation it is impossible to draw any immediate conclusions from the observed morphological changes in the cell which it causes.

Picric acid.—Picric acid fixation for permanent mounts was done with a saturated solution used at room temperature and at 45-50° C. Observations on the immediate effects of fixation were made with a saturated solution used at room temperature.

Fixation with picric acid was very rapid, occurring in less than a minute, insofar as visible changes are concerned. Death was instantaneous, and cytoplasmic shrinkage was very great. Nuclear shrinkage was somewhat smaller than cytoplasmic shrinkage. The nuclear membrane was homogeneous after fixation. It did not undergo shrinkage, and remained homogeneous and refractive. The peripheral ground-plasm was formed as a rather coarse yellow precipitate. The spherules disappeared during fixation, and the granules were usually obscured by the precipitated ground-plasm. The endosomes were homogeneous, and appeared to be well preserved. The central ground-plasm was precipitated as a coarse material, usually drawn away from the peripheral region rather considerably. This tendency towards separation of the central and peripheral regions, noticed in many other fixatives, was accompanied by an unusual condition. The endosomes, which usually remained at the surface of the peripheral region when the two were separated in other fixatives, consistently clung to the central region and were drawn away from the peripheral zone in picric acid.

In permanent preparations the nuclear membrane was homogeneous

and refractive, and invariably acidophilic. The membrane appeared to be thicker in nuclei fixed with picric acid than with other fixatives. The peripheral ground-plasm was drawn away from the central region, and appeared to be finely granular. Imperfectly preserved peripheral spherules were occasionally found imbedded in the ground-plasm, but they were never present in large numbers as in living nuclei, and usually were absent. Basophilic granules were present, staining darkly with haematoxylin and safranin. The endosomes were well preserved. They were homogeneous, distinctly outlined, and almost hyaline when completely decolorized. In many cases a more basophilic cortical substance was observed in the endosomes. The central ground-plasm was separated from the peripheral region, and appeared as an acidophilic, reticular region. A centriole was occasionally observed. The hyaline body was never prominent, but traces of that structure were occasionally found. When present it tended to be slightly acidophilic. Dividing forms were not numerous, so the structure of the dividing nuclei could not be studied very thoroughly. The chromosomes appeared to be rather poorly preserved, with indistinct outlines and evidences of fusion, particularly in the washed preparations. They were acidophilic, being rapidly decolorized. No dividing nuclei were found in the Feulgen preparations.

Picric acid precipitates proteins in the same way that other compounds containing complex anions act. The anion forms a chemical compound with the protein; in the case of picric acid, a protein picrate. Picric acid is said to have no effect on lipides, but to preserve albumin, globulin, nuclein, and nucleic acid. The precipitate of nucleic acid is soluble in water, according to Mann (1902). Jones (1920) says that picric acid precipitates only protein from the nuclein solutions, leaving the nucleic acid in solution. The failure to precipitate nucleic acid may very possibly be involved in the apparent poor preservation of the chromosomes by picric acid. Since the endosomes appear to be very well preserved, it seems to indicate that they are precipitated entirely, and not in protein and nucleic acid fractions. If they are precipitated in protein and nucleic acid fractions, the nucleic acid must dissolve very quickly, for no indications of a positive Feulgen reaction was obtained in the endosomes, even when the contact with water was reduced to a minimum.

Osmium.—Fixation for permanent mounts was accomplished with osmic vapor used for 45 seconds to one minute, and a 2 per cent solution of osmium tetroxide at room temperature. For the study of the immediate effects of fixation the 2 per cent solution was used at room temperature.

At the moment the **fixative** was applied the first group of visible alterations occurred instantaneously. There was no noticeable shrinkage

of cytoplasm or nucleus. The cytoplasm remained very lifelike, and the nucleus retained its normal size and shape. The nuclear membrane became noticeably darker and was less refractive. It gave an added indication of an alteration in its substance by a marked affinity for methyl green. It remained homogeneous, however. The peripheral ground-plasm remained homogeneous after fixation. For about ten minutes the spherules were visible, not altering their appearance in any way. After this they gradually disappeared, and finally were entirely dissolved. The peripheral granules became a little more prominent and refractive during fixation. For the final appearance of the nucleus to be attained (Fig. 37) required, on the average, about fifteen minutes. The central region was precipitated in a finely granular condition in all cases. A centriole was never observed, possibly because of the granular nature of the precipitated central ground-plasm. The hyaline body was distinct after fixation of nuclei in the late kinetophase or early interphase (Fig. 37). It was homogeneous and retained its characteristic position at one pole of the central region. Unlike its appearance in many other fixatives, especially when studied in permanent mounts, its outlines were regular and distinct. It had a slight affinity for the basic dyes. The endosomes were coagulated by osmium, usually appearing to be perfectly homogeneous, but in rare cases of large endosomes, showing a vacuolated inner structure. They were invariably distinctly basophilic, staining deeply with methyl green.

In permanent preparations the nuclear membrane remained homogeneous and basophilic. The peripheral ground-plasm was homogeneous, and stained lightly with basic dyes before differentiation. The basic dyes were rapidly extracted, and the ground-plasm stained darkly with acid dyes. Peripheral spherules were not found in nuclei fixed with osmium tetroxide solution, but occasionally could be found very imperfectly preserved and much misshapen in preparations fixed with the osmium vapor. The peripheral granules were invariably basophilic, but never so deeply basophilic as the endosomes. The endosomes were not very well preserved, and in many cases the outlines were rather indistinct, especially in nuclei fixed with osmium vapor. The remnants of such endosomes stained with the basic dye. In endosomes fixed with the solution, the shape was frequently well preserved, and the endosomes showed a distinct differentiation of an inner less basophilic material and an outer more basophilic material. The inner substance was not infrequently gathered in vacuoles in larger endosomes. The central region was well preserved. The ground-plasm was precipitated in fine particles which did not form a reticulum. In some nuclei the basophilic centriole could be seen. A hyaline body was not observed in most nuclei, but in some

cases it was visible in an incomplete form. Its reaction to stains varied somewhat in different nuclei, ranging from slightly basophilic to somewhat acidophilic.

Osmic fixation is thought to occur in two steps. The primary action, described by Berg (1927), involves a combination of the molecule with the protein amino-groups. The second action is associated with a gradual oxidation of the compound formed and is accompanied by a blackening of the tissues and a reduction in their stainability. Osmium preserves things in a very lifelike state, especially the fats and lipides. Baker (1933) reports that cells are more lifelike after osmium fixation than any other simple fixative. It was the more remarkable in view of these statements, to observe that the nucleus was not as lifelike after fixation with osmium as after formaldehyde. Cytoplasmic fixation was superior to that observed for any other simple fixative. Except for the refractive peripheral spherules and the central region, osmium fixation is rather lifelike, while the nucleus is still lying in the fixative. New unlikelike appearances creep in during the washing and staining procedures, causing the final appearance in permanent mounts to be quite different from that of the living amoeba.

B. COMPOUND FIXATIVES

As most of the changes in nuclear appearance resulting from fixation with the compound fixatives survived the washing, dehydration, and staining procedures involved in making permanent slides, only the observations made on nuclei during fixation are given below. A few detailed differences may be found in the discussion of nuclear morphology in the trophic nucleus in a later section. Many of the effects of fixation with compound fixatives showed rather clearly a summation of the effects of the reagents composing them.

A variety of compound fixatives was tried, but for most of the descriptive work, at least, six were used almost to the exclusion of the others. These were Gilson-Carnoy, Schaudinn, Carnoy, Bouin, Zenker and Flemming. A brief discussion of these will precede the observations of fixation.

Gilson-Carnoy, a powerful fixative composed of a saturated solution of mercuric chloride in six parts of absolute alcohol, three parts of chloroform, and one part of glacial acetic acid, is the most vigorous fixative used in this study. It is generally recognized as an extremely penetrating fixative, and is not recommended for cytological work on delicate structures. The chief objection to it given in most technique manuals is the shrinkage which it is reputed to cause. It is said to leave the nucleus and cytoplasm in a most unlikelike condition.

Schaudinn is composed of 2 parts of a saturated solution of mercuric chloride and one part of absolute alcohol, plus one to five per cent of glacial acetic acid. In this study the acetic acid was varied between one and two per cent. This rather strong and penetrating fixative is an active precipitant of almost all the substances found in the cytoplasm and nucleus. Although it is widely used among protozoologists it is not popular with cytologists. Baker (1933) does not even mention it. McClung (1938) recommends it as a standard routine fixative for protozoan work, but not to be used for special investigation without supplementation with other fixatives. Langeron (1925) similarly relegates its use primarily to protozoan work, but recommends either alcoholic or aqueous Bouin's as being equally satisfactory.

Carnoy is composed of 3 parts of absolute alcohol and one part of glacial acetic acid. It is a strong precipitant and penetrates rapidly. Baker (1933, p. 65) says, "The fluid is a rational one, for the acetic prevents the shrinkage and extreme hardening which would be caused by the alcohol. The alcohol fixes the cytoplasm and the acetic acid the nucleoproteins." According to Baker it dissolves lipides, and precipitates glycogen. It is a good fixative for chromosomes but cannot be used for Golgi and mitochondria. Most of the remainder of the handbooks on microscopical technique recommend Carnoy as a rather good fixative for nuclear detail if accompanied by fixatives of other types.

Aqueous Bouin, composed of 25 parts of 40 per cent formaldehyde, 5 parts of glacial acetic acid, and 75 parts of a saturated solution of picric acid has long been recognized as one of the most dependable of general fixatives. Baker (1933, pp. 65, 66) remarks, concerning the general properties of Bouin as a fixative, "Mitochondria are not usually fixed. The fluid penetrates quickly and fixes evenly. . . . The chromosomes are no doubt fixed mainly by the acetic and the formaldehyde probably restrains the too coarse precipitation of the cytoplasm by the picric and of the nucleoproteins by the acetic, while the picric gives a sufficiently soft consistency for easy sectioning and makes staining easy."

Zenker is not a standard cytological fixative. It is not mentioned by Baker (1933) and is but briefly mentioned in most other handbooks of cytological technique. It is composed of a solution of 2.5 per cent potassium bichromate, 1 per cent sodium sulphate, 5 per cent mercuric chloride, and 5 per cent acetic acid. It has not been used extensively in studies on the nucleus in Sarcodina, but has been highly recommended as a fixative for studies of the cytoplasmic fibrils and other structures in ciliates.

Flemming, composed of 15 parts of a 1 per cent solution of chromic acid, 4 parts of a 2 per cent solution of osmium tetroxide, and 1 part of

glacial acetic acid is one of the most widely used and best liked fixatives. Baker (1933) observes that it frequently does not fix evenly. This difficulty was encountered in colons preserved whole for sectioning, when the amoebae along the margin of the colon were much more satisfactorily preserved than those in the center. Baker explains its action in the following way (p. 68), "The osmium gives a homogeneous fixation of the cytoplasm, prevents too crude a precipitation of the nucleoproteins of the interkinetic nucleus, and preserves and blackens fats, while the acetic acid and chromic preserve the chromosomes admirably. The chromic further gives sufficiently firm consistency and facilitates the staining of chromosomes with the basic dyes." In preparations made for this study Flemming fixation was exceptionally good in most respects.

With all of these fixatives death was instantaneous. The effects of fixation on the various nuclear elements, with very few exceptions, reached completion so rapidly that each structure had to be studied separately and observed many times in order to gain a complete view of what happened during fixation. Visible alterations were usually complete after the first five to fifteen seconds, except in Zenker and Flemming, when some of the effects were quite deliberate.

The strong fixatives, Gilson-Carnoy, Schaudinn, and Carnoy, form a coarse cytoplasmic precipitate. Alveolation is somewhat less marked in Carnoy than in the other two strong fixatives. Cytoplasmic alveolation was still less developed in Bouin. A very coarse cytoplasmic precipitate was formed during fixation with Zenker, but alveolation was very slight. Cytoplasmic fixation was most nearly lifelike with Flemming, where a fine precipitate and almost no alveolation was the rule. Cytoplasmic shrinkage was very great with Gilson-Carnoy and Schaudinn. Carnoy and Bouin bring about much shrinkage, although less than the preceding two fixatives. Shrinkage in Flemming and Zenker is extremely small. It appears from these results that there is very little correlation between the size of the particles precipitated and the degree of shrinkage and alveolation. As might be anticipated, however, there is a rather direct correlation between the amount of cytoplasmic shrinkage and the degree of alveolation.

Nuclear shrinkage is not directly correlated with the cytoplasmic shrinkage. The greatest shrinkage of the nucleus was observed consistently in Gilson-Carnoy, Schaudinn, and Flemming. Carnoy caused marked shrinkage, but less than the above-mentioned fixatives. The smallest nuclear shrinkage was caused by Bouin and Zenker fixation. The large amount of nuclear shrinkage during Flemming fixation was surprising in view of its accepted excellence as a nuclear fixative. Although repeated many times, the same amount of shrinkage was invariably

found. In spite of this, the spatial relationship of the various nuclear elements remained unchanged, and accurate presentation of nuclear structure invariably resulted from Flemming fixation.

Visible alterations in the nuclear membrane were very slight during fixation. The advancing wave of fixative always elevated the cover slip slightly, so that the nucleus was less compressed and the membrane appeared somewhat thicker. Because of this it was impossible to estimate accurately the shrinkage or swelling of the nuclear membrane during fixation. The highly refractive membrane always appeared somewhat less refractive after fixation with Gilson-Carnoy, Schaudinn, and Flemming fixatives. Part of this loss in refractivity of the membrane undoubtedly came as a result of the increased refractivity of the cytoplasmic substances. However, the other fixatives used, which also caused a change in the refractivity of the cytoplasmic substances, left the nuclear membrane almost unchanged. For this reason it appears probable that there was some direct effect of the first three fixatives on the nuclear membrane. A definite precipitation of the substances composing the nuclear membrane was never observed. The membrane remained clear and hyaline in all cases. During the shrinkage of the nucleus it was hoped that some evidence of the hyaline cytoplasmic membrane investing the nucleus, described by Bütschli (1878), might be found. Careful observation failed to reveal any trace of this structure. The nuclear membrane remained homogeneous in all fixatives, and the bilamellar structure of the membrane described by Schubotz (1905) was never observed. Striations, possibly canals extending through the nuclear membrane, as described by Sassuchin (1930) were also looked for in vain. The nuclear membrane in the fixed state was invariably acidophilic, or, at least, showed no affinity for methyl green or acetocarmine beyond that showed by the cytoplasm, unless fixed with Flemming. After Flemming fixation the membrane was distinctly colored by methyl green, and somewhat less so by acetocarmine. Many times the stained membrane was almost as dark as the endosomes. A similar affinity for basic dyes was observed in the nuclear membrane of nuclei fixed in Flemming and Champy in permanent slides. Among the simple fixatives, osmium showed a very distinct tendency to cause the membrane to become basophilic, and chromic acid, also, gave the membrane a less marked tendency to be stained with haematoxylin. Baker (1933) suggests that the chromic acid causes an increased affinity of tissue for haematoxylin by a mordanting action. This is even more marked with mitochondria and other cytoplasmic structures. In view of the mordanting effect of chromic acid which has been postulated, the writer is inclined to explain the basophilic affinities of the Flemming-fixed nuclear membrane as being caused by

osmic acid. It seems probable that it depends on the nature of the additive compounds formed by osmium and the substances composing the nuclear membrane, which Baker (1933) believes are formed.

Fixation of the peripheral zone causes very profound changes in its appearances. The strong alcohol-acetic-sublimate fixatives precipitate the peripheral ground-plasm, almost invisible in the living nucleus, in fine particles which gather in irregular, flocculent masses. Only rarely is a reticulum formed. In all cases observed, this tendency was most marked in Gilson-Carnoy and Schaudinn, followed by Zenker, Bouin, Carnoy, and Flemming in approximately that order. These effects, although very obvious and easy to observe, probably involve many diverse chemical and physical reactions of fixative and substances comprising the ground-plasm. Certainly the original colloid is greatly altered even in Flemming, when a coarse precipitate is formed which is almost evenly distributed throughout the peripheral region. To what extent the results observed can be traced back to the effects as seen in the observations of the effects of simple fixatives is difficult to say. Those substances which cause the greatest degree of accumulation of particles in flocculent masses in the fixatives studied must be sought in the components of Gilson-Carnoy, Schaudinn, and Zenker, and should be absent in Flemming. No such substance can be found, for there is no single substance present in the first three and absent in the last fixatives. It seems probable that mercuric chloride, present in the vigorous fixatives, does not bring about the formation of the flocculent masses, since when used alone it leaves the peripheral ground-plasm in a comparatively homogeneous condition. Similarly alcohol, which is found in the first two fixatives, did not cause such a flocculent mass of substance to be formed when used alone. Acetic acid, however, when used in higher concentrations, did bring about the appearance in question, and may be the most important factor in causing it in Schaudinn and Gilson-Carnoy. Probably in Zenker fixation, the acetic effect is aided, at least, if not replaced, by the effect of the potassium bichromate, which in several attempts also caused a vigorous precipitation, which tended to be accompanied by the arrangement of the particles in flocculent masses. The action of the acetic may be hindered in Carnoy by the greater proportion of alcohol and by the absence of water. The Flemming effect may be caused by the low percentage of acetic, while in Bouin it is possible that the formaldehyde hinders the acetic effect. Until further work of a more detailed nature can be undertaken, the complete explanation of the effects of the various compound fixatives cannot be satisfactorily explained, and the above must be classed as suggestion rather than explanation.

Lying imbedded in the precipitated peripheral ground-plasm are the

peripheral spherules and granules. The spherules are dissolved, partially or entirely, by most of the fixatives, or are imperfectly preserved. Gilson-Carnoy and Schaudinn appeared to cause the spherules to dissolve, or, perhaps, completely obscured the remnants of the spherules in the mass of ground-plasm. Carnoy caused a partial solution of the spherules. Flemming fixation was accompanied by a loss in refractivity of the spherules, and in the unstained nucleus the spherules were almost obscured. Even Flemming fixation failed to preserve the spherules entirely. In Bouin fixation the spherules disappeared very rapidly, so that in less than a quarter of a minute after the fixative had begun to act the spherules were completely dissolved. With Zenker the spherules also dissolved, but in a very deliberate fashion. When the fixative first came in contact with the nucleus the spherules became less refractive. Then, after from five to eight minutes a diminution in the diameter of the spherules became noticeable. In about ten minutes the spherules were almost completely dissolved and shortly thereafter they were no longer visible. Attempts to understand the action of the compound fixatives with the use of the observations made on the action of the simple fixatives has not been entirely satisfactory in the case of the peripheral spherules. Mercuric chloride, osmium tetroxide, and chromic acid cause the solution of the spherules, as do the high grades of acetic acid. The other fixatives either preserve them imperfectly or leave them in a condition in which they may be partially destroyed by the technical procedures followed during the preparations of permanent mounts. Formalin alone causes a lifelike preservation of the peripheral spherules. In view of the above, it is easy to explain why the various compound fixatives dissolve, or fail to fix, the spherules, for they all contain at least one substance inimical to the spherules. The real difficulty comes in explaining the action of Flemming (Fig. 39), which, although it contains chromic acid and osmium tetroxide, does not dissolve the spherules. This seems to indicate that the spherules are perhaps precipitated by low grades of acetic in an insoluble form, an idea which the study of the action of acetic alone does not entirely controvert. If this is the case, however, it is not clear why the same effect does not occur in Zenker fixation. At present, no explanation can be offered for these results.

Observations on the peripheral granules can be made very briefly. With the compound fixatives, generally speaking, the granules become more refractive during fixation. This is, in the case of the alcohol-acetic-sublimate fixatives, at least partially obscured by the heavy precipitate of the ground-plasm. Careful study, however, almost invariably shows the granules to be lying interspersed throughout the ground-plasm. In all cases the granules are lightly stained by methyl green and acetocarmine.

The fact that the granules are visible, although with difficulty, in the living nucleus, and that the same granules have been observed to become more numerous and refractive during fixation while the peripheral spherules disappear indicates very clearly the fact that there are two definitely different types of inclusions in the peripheral region of the nucleus, confirming the observations of Janicki (1909) and Kudo (1926). This point has been the source of some difficulty in the past (see p. 32). Janicki contended that there were two types of inclusions, one of which dissolved during dehydration. Kudo likewise considered that there were two types of inclusions, one of which dissolved during fixation. Basophilic ones, invisible during life, were believed to appear during fixation to give the peripheral region its characteristic stippled appearance in permanent mounts. Elmassian (1909), Mercier (1910), and Morris (1936) appear to have noticed only one kind of peripheral inclusion, believing that the spherules and the granules were identical. Sassuchin (1936) mentions two types of inclusions distinguishable on the basis of staining reaction, probably referring to the peripheral spherules and granules. Since it has been shown in the present study that (1) the peripheral granules and spherules are both visible in life in favorable nuclei, (2) the peripheral spherules are resistant to staining when present in fixed nuclei, (3) the peripheral granules are smaller than the spherules, more irregular in shape, basophilic, and distributed differently in living and fixed nuclei, and (4) the peripheral spherules have been observed during fixation in the process of dissolving in nuclei in which the granules were clearly visible, it seems that the thesis of Kudo can be confirmed completely. It may be appended that the spherules may dissolve, at least partially, during the preparation of the permanent slides, but that this appears to occur in water and not in alcohol, as suspected by Janicki.

The endosomes, invisible in life or visible as indefinitely outlined shapes, become much more refractive during fixation with all compound fixatives. They are invariably precipitated almost instantaneously and undergo no further visible changes. The amount of shrinkage could be determined in but one nucleus in which the endosomes were distinctly visible in the living state, and therefore was not typical. This nucleus, fixed in Zenker, showed very little shrinkage, and the endosomes underwent no measurable shrinkage. The endosomes, homogeneous and hyaline after all fixatives when comparatively small, were frequently divided into two types of substances in the nuclei in which large endosomes prevailed. In this case the cortical portion of the endosomes was more dense and refractive, and the inner portion more dispersed and less refractive. The inner substance was sometimes collected in vacuoles in

the largest endosomes. The endosomes were invariably basophilic, staining rather deeply with methyl green and acetocarmine. In nuclei fixed with Zenker the cortical and inner types of substances were particularly well shown, and the denser substance appeared to be more basophilic, even in the temporary slides stained with acetocarmine. Endosomes fixed in the elongate strand condition showed no inner structure. Since there were so few visible differences in endosomes fixed by the various simple fixatives it is not possible to speculate on the part the simple fixatives play in bringing about the precipitation of the endosomal substances.

Because of the increased opacity of the peripheral material resulting from precipitation of the ground-plasm, the central region could be studied in detail in but a few favorable cases. The central ground-plasm appeared to be precipitated as a homogeneous region by Gilson-Carnoy and Zenker. Carnoy-fixed nuclei had a finely granular, amorphous, or indistinctly reticular central region. Schaudinn contracts the central region into a dense mass of rather coarse particles in which a hyaline body may occasionally be seen. Flemming, like Schaudinn, induced a considerable amount of shrinkage of the central region, which although less marked than in Schaudinn, separated the two ground-plasms at the margin of the peripheral region. The central ground-plasm precipitate was rather coarse. When fixed in the late kinetophase or early interphase condition the Flemming-fixed nuclei frequently show well-preserved hyaline bodies at one pole of the central ground-plasm (cf. Figs. 38 and 39). The hyaline body, invisible in life, is homogeneous and refractive in the fixed nuclei, with smooth outlines. It was always found at one pole of the ground-plasm, and with some practice could be distinguished from the endosomes without staining with methyl green or acetocarmine. In stained nuclei it was invariably more slightly basophilic than the endosomes. The ground-plasm was always acidophilic, although during early interphase, when the ground-plasm lay near one pole of the nucleus with the hyaline body attached to it, small granules could be seen which appeared to be slightly basophilic. The centriole could be seen so rarely in nuclei immediately after fixation that no systematic observations were attempted for it. As with the endosomes the central region presents so few differences in appearance which are characteristic in the studies with simple fixatives, it is impossible to speculate concerning the part the various simple fixatives play in bringing about the action of the compound fixatives. The hyaline body, however, can be analyzed to a certain extent. It is fixed by osmium, and is visible after fixation with alcohol and mercuric chloride. In the case of alcohol and mercuric chloride, the precipitated hyaline body appears to be readily soluble in

water, for it disappears during the preparation of permanent slides. In the compound fixatives, it was seen only in nuclei fixed with Schaudinn and Flemming. With Schaudinn fixation, it is not insoluble, and so disappears during the after-treatments leading to the preparation of permanent slides. In Flemming-fixed nuclei, however, it is present in permanent mounts. This parallels closely the observations made with simple fixatives. It would appear that acetic acid is distinctly inimical to the precipitation of the hyaline body in larger quantities, for in Gilson-Carnoy, containing the alcohol and sublimate necessary to precipitate it in a soluble form it was never seen. It was never found in Zenker-fixed nuclei, which also suggests that it may possibly be destroyed by potassium dichromate. Not enough work was done with fixation resulting from potassium bichromate alone to make a comparison on this point, although a hyaline body was never seen in dichromate-fixed nuclei. It may be said that of the various simple fixatives tried, osmium is the only one to precipitate the hyaline body in an insoluble form, and that compound fixatives which contain osmium are most likely to preserve it in a recognizable form. In several nuclei fixed with Champy the hyaline body was present, which serves to strengthen this supposition.

XII. NATURE OF THE ELEMENTS OF THE TROPHIC NUCLEUS

IT APPEARS from the preceding descriptions that there are a number of distinctive elements occurring in the nucleus of *E. blattae*, visible in living or in fixed amoebae. In order to summarize the results of the observations made on the various types of material, the following conclusions and inferences may be given.

Nuclear membrane.—The nuclear membrane is a homogeneous structure in both living and fixed conditions. In rare cases after Gilson-Carnoy fixation it may appear superficially to be bilamellar in structure, but this condition is encountered so rarely that it may be assumed with safety that it is abnormal, even though it is unaccompanied by definite morphological evidences of degeneration. It is not probable that it is entirely an effect of fixation. The fact that Schubotz (1905) noticed in an unpreserved, dead organism a double nuclear membrane appears to indicate that the bilamellar condition may exist without fixation, and the rarity of its occurrence even in material fixed in Gilson-Carnoy suggests that it was not the fault of the fixative entirely. A stratified appearance may be observed in almost all nuclei either in life or in fixed condition. This appears to be due entirely to the diffraction of light, and is not considered to be an indication of structural lamination. In no case has a

delicate membrane between the cytoplasm and the nucleus, such as that described by Bütschli (1878), been observed. No suggestions concerning the structural basis of Bütschli's description can be made at this time. In many amoebae the nuclear membrane is drawn out into a beak-like projection, as observed by all previous investigators. This appears during the late division stages as a remnant of the inter-nuclear strand, and gradually disappears after division, as stated by Janicki (1909). Janicki's statement that the nuclear membrane is thinner at the locus of the extension appears to be true during the time it is prominent, but as it becomes smaller it forms a small rounded prominence on the membrane in which the wall of the nucleus is thickened. Concerning the striations of the nuclear membrane, described by Sassuchin (1930), who interpreted the striations as canals leading through the nuclear membrane, little can be said at the present. At no time have such striations been seen in bright or in dark field. Fixed nuclei, also, are without such striations, insofar as could be determined with the optical equipment used. In a few nuclei stained with safranin, striations were produced by the arrested diffusion of the stain through the membrane, but these do not appear to be analogous to those described by Sassuchin. In its reactions to stains the nuclear membrane is almost invariably acidophilic, although it acquires a slight affinity for basic dyes after treatment with osmic fixatives. In the latter case this is most marked with haematoxylin fixation, but may also be noticed after staining with methyl green, acetocarmine, and to a slighter degree, with safranin. The basophilic properties are apparently the direct result of the formation of additive compounds with the osmium, or possibly with chromic acid occurring in the fixative and the substance of the membrane. The fact that all osmium fixatives used gave this effect strengthens the view that it is osmium which forms the additive compounds.

The nuclear membrane yields typical protein reactions to the various treatments to which it was subjected. It was precipitated in an insoluble condition by all of the simple fixatives tried, except, possibly, with dioxane, which appears to have caused a partial dissolution of the membrane. It was slightly soluble after fixation in dilute acetic acid, in which case heat apparently aided in the precipitation, since hot acetic gave a more complete precipitation than cold acetic among the lower grades. In its general reactions it closely resembled the complex cytoplasmic proteins. That it is unlike any of these appears certain, although the difference may conceivably be a physical rather than a chemical one. It is interesting to note that the membrane never lost its characteristic hyaline appearance even in the most vigorous fixatives. This suggests that the membrane is not a pure protein, or that it may possibly be a gelled

colloid of very dense structure. With the present knowledge of the physical condition of the precipitated proteins and protein compounds, no more definite conclusions can be drawn.

Peripheral ground-plasm.—In the living state the peripheral ground-plasm is hyaline and clear, containing numerous peripheral spherules and peripheral granules. Bütschli described it as a finely granular-reticular region. His work was done with living nuclei only. The reticular appearance which he mentioned was not demonstrable in the living nucleus. The reticular appearance frequently seen in fixed preparations is thought to be the result of fixation shrinkage, and a general relationship of the size of the interstices of the reticulum and the amount of shrinkage of the ground-plasm appears to support this view. Baker (1933) also supports the view that the reticular appearance of the karyolymph in metazoan cells is caused by fixation. He says (p. 15), "His [Tellyesniczky] reasons for disbelieving in the meshwork in the nucleus were (1) that it is invisible during life; (2) it does not appear after fixation with those fixatives that are not protein precipitants; (3) that it does appear after fixation with protein precipitants; and (4) that in appearance it resembles a protein coagulum. . . . There seems little doubt, however, that the ground substance of the nucleus is structureless, and that the network or spongework is an artifact produced by fixation." Sharp (1934) appears to agree with Baker on this point. After most fixatives the peripheral ground-plasm is acidophilic, but after Zenker fixation, there is a much heightened affinity of the ground-plasm for the basic dyes. This is noted also, although to a somewhat slighter degree, after fixation in Flemming and Champy. This may possibly be traced to the chrome compounds which may have a mordanting effect, especially for haematoxylin.

It may be mentioned here that in no case do the peripheral and central ground-plasms appear to be continuous. They may be in contact for a lesser or greater portion of their margins, but invariably present some visible signs of differentiation. This may appear as a physical difference in the precipitated particles with respect to size, as in Gilson-Carnoy fixation, in which the central ground-plasm is composed of very fine particles and the peripheral ground-plasm of coarser ones. It may appear as a difference in stainability, as in Carnoy, when the peripheral net is acidophilic, and the central net somewhat basophilic, or in the size of the meshes of the nets, as is the case in Flemming, Carnoy, Schaudinn, etc. All of these point to the conclusion that the peripheral and central ground-plasms are to be considered as distinct substances, differing in physical, if not in chemical, nature, and in no case are to be considered as continuous, as suggested by Elmassian (1909).

The peripheral ground-plasm appears to be of protein nature, since it

is precipitated with protein precipitants, and shows other typical protein reactions. Its failure to react with basic dyes suggests that it is not combined with nucleic acid in the form of a nuclein or a nucleoprotein. This interpretation is further suggested by the fact that the peripheral ground-plasm is very rapidly dissolved with pepsin-hydrochloric acid. At present it appears impossible to come to any conclusions concerning its chemical nature, but it is inferred that the ground-plasm is a rather complex mixture of substances, with the basic material being a protein which is normally in the gel phase during interphase, and appears to shift to the sol phase during kinetophase. This protein material appears to be similar to, but not identical with, the substances of like nature occurring in the cytoplasm, for there is a consistent visible differentiation between these two protein substances.

Peripheral spherules.—In the living nucleus the peripheral ground-plasm contains large numbers of highly refractive spherules. These are clumped at one end of the nucleus during the early interphase where they frequently remain long after the other nuclear elements have regained their original concentric organization. During fixation the spherules react in extremely diverse ways. With some, Bouin's, for example, the spherules rapidly dissolve, with others, such as Zenker, they dissolve very slowly, and in a few cases they are not changed in appearance, as in formaldehyde. They are quite resistant to staining with all stains. In safranin preparations, following a Flemming fixation, the remains of the spherules are colored a very light pink shade. This is the only known case where they react positively with a basic dye. Occasionally they are lightly stained with acid dyes. It is not impossible that these observed staining reactions are actually accumulations of stain at the surface of the spherules. The spherules have been the source of much difficulty in the past. Schubotz (1905), who was the first to describe them, was uncertain as to whether or not they were visible in the fixed nucleus. Elmassian (1909) believed that they were identical with the granules he observed in the fixed nucleus. Janicki (1909) stated that they were soluble in alcohols and appeared only in preparations which had undergone rapid dehydration and then were present in a partially dissolved condition. Mercier (1910) described them from the living nucleus but did not definitely link them with the granules seen in fixed nuclei. Kudo (1926) stated that they dissolve in the process of fixation and are replaced by chromatin granules in the fixed nucleus. Morris (1936) stated that the refractive spherules in the living nucleus were identical with the chromatic ones of the fixed and stained nuclei.

On the basis of the observations made on the fixation of nuclei, it seems evident that the peripheral spherules are soluble in some fixatives,

as stated by Kudo, but not in all of them. In those fixatives in which they are not dissolved, some preserve them well, and others do so but poorly. The spherules do not appear to be soluble in alcohol, as suggested by Janicki, but are actually preserved, although not perfectly, by absolute alcohol. It appears that during the dehydration process the spherules, if partially destroyed, are dissolved by the water rather than by the alcohol. It can be stated without reservation that the spherules and granules are not identical. In favorable cases both are visible in the living nucleus, and in a few cases, both are visible in fixed nuclei. When they are both present in the fixed nucleus, the spherules are resistant to staining, while the granules are basophilic. It seems evident that the conclusions reached by Kudo and Janicki were essentially correct.

In their reactions to most of the techniques tried, the peripheral spherules gave results which were rather dubious. They were coagulated by heat, it appears, since in some cases the fixation of the spherules was improved by heating the fixative. They were also partially coagulated by alcohol. Although seemingly partially soluble in glacial acetic acid, there was no evidence to show that they were soluble in dilute acetic acid, and appeared to be insoluble in alcohol following treatment with dilute acetic acid. They were insoluble in picric acid and soluble in chromic acid. Mercuric chloride left them in a rather insoluble condition in saturated solution, insofar as water and alcohol are concerned, but the spherules dissolved in the saturated sublimate solution if left in it long. These reactions do not fit perfectly with any type of chemical substance with which the writer is familiar. In general, however, they appear to show some relationship to the phospho-globulins, but until more information is available they cannot be placed in this group. It is interesting to observe that if they should belong to some chemical group similar to the phospho-globulins they might serve as a source of paranucleic acid and albumins, and thus supply material for the rest of the nuclear elements. Janicki (1909) has suggested, without offering any significant evidence for its support, that they represent a reserve food supply for the nucleus. If the spherules are acting as a source of phosphorous-containing compounds to be utilized in the production of nucleic acid this would support his ideas. It is interesting in this respect, to observe that during the early precystic development, when the spherules are disappearing (see p. 114), there is a distinct increase in the amount of nucleic acid present in the nucleus, as measured by the Feulgen nucleal reaction. There is no evidence, however, that the appearance and disappearance of the Feulgen-positive substances in the central region of the nucleus during division in the trophic stage is aided in any way by the refractive spherules.

Peripheral granules.—Although never prominent, the peripheral granules may be observed in favorable living nuclei. They are usually obscured partially or wholly by the peripheral spherules. In fixed nuclei the granules are basophilic, but remain uncolored by the Feulgen reaction. Schubotz (1905) reported that they were colored orange in Flemming triple preparations, but in such preparations made for this study they were colored a light red, indicating basophilic properties.

Up to the present time there is little evidence to indicate the function of the peripheral granules in nuclear activities. Janicki (1909) suggested that the peripheral granules served as a supply for the endosomes and that the endosomes grew by the addition of basophilic substances from the granules to their surface. The present study has failed to gain any evidence either for or against this interpretation of the granules' function.

The peripheral granules are precipitated by nearly all reagents used. They were poorly preserved by low grades of alcohols and acetic acid, and osmic tetroxide fixation leaves them in a somewhat indeterminate state. They are digested in pepsin-hydrochloric acid and are soluble in 10 per cent solutions of sodium and potassium chloride. They are basophilic, but less so than the endosomal material. In their general reactions they appear to be closely allied to the nucleins. The uncertain knowledge of nucleins, due to the great variation in their chemical make-up, makes it impossible to go beyond this point in their analysis at this time.

Endosomes.—In the living nucleus the endosomes cannot be studied, as they are visible as indefinite shadows, or wholly invisible. Fixed nuclei are characterized by more prominent endosomes. As they are basophilic they show up well in permanent preparations. In haematoxylin or safranin they stain very dark, and after strong alcoholic fixatives, sublimate fixatives, or Zenker, the inner structure occasionally becomes apparent. The larger endosomes present a typical appearance. There is a dark-staining region in the cortical zone, which represents a shell of basophilic material. This contains a more lightly-staining substance which may fill the whole interior of the endosome, or be lodged in vacuoles. In many cases a central basophilic granule lying at the very center of the endosome can be observed. Janicki (1909) observed that large endosomes are frequently built as vacuolated structures, and Mercier (1910) and Kudo (1926) observed similar structure in some endosomes. Morris (1936) pointed out that there was usually a basophilic cortex and a more lightly-staining interior. The central granule of basophilic material does not appear to have been mentioned, and its significance is not understood. The dual nature of the endosomal material seems quite evident, although all of its implications are not yet understood. The lightly-staining material may be formed from the basophilic portion, which may

account for the growth of the endosomes during the late interphase period, but the evidence for this point is very slight. There is no reason to believe with Janicki (1909) that the endosomal growth during interphase occurs as a result of the endosome taking up substances from the central region, since in reaction to fixatives and stains the substances are distinctly different. Although intensely basophilic, the endosomes do not react with the Feulgen reagents at any time during interphase or kinetophase.

The endosomal variation in shape, size, and number is very striking. Shape varies from elongate to the predominantly spherical types, with various intermediate shapes. The number of endosomes varies from about five or six to twenty-four or more. Morris (1936) points out that the endosomal number approximates the chromosomal number. The wide range of variation and the fact that there is some indication of a reduction of endosome number during the late interphase period suggests that this similarity between average number of endosomes and approximate number of chromosomes is coincidental rather than indicative of a true correlation.

The cortical, basophilic, portion of the endosomes is well preserved by mercuric chloride, chromic acid, and 10 per cent acetic acid. It is less well preserved by alcohol, osmium, and formaldehyde, and appears to be irregular and doubtfully preserved in glacial acetic acid. The substance is rather resistant to digestion when put in pepsin-hydrochloric acid solution, but is broken down after some time. It is soluble in the 10 per cent solutions of sodium and potassium chlorides. These reactions suggest that we have to do with a nucleoprotein. The poor preservation of the endosomes in stronger acetic acid solutions is believed to be primarily the result of the action of the acetic on the inner, more lightly-staining material. The basophilic part of the endosomes appears to agree in all particulars with the expected reactions of nucleoproteins if this view is maintained.

The inner endosomal material is less easily determined. It is preserved very well in picric acid, chromic acid, and mercuric chloride, and less well by alcohol, glacial acetic acid, osmium, and formaldehyde. It is preserved in dilute acetic acids, however. It seems to be dissolved by 10 per cent solutions of sodium and potassium chlorides, and is rapidly attacked by pepsin-hydrochloric acid digestion. It seems possible that it may represent a product of the disintegration of the basophilic outer portion of the endosomes, which might suggest that it is a nuclein of some kind. However, the acetic acid reaction argues against this interpretation. Mann (1902) showed that nuclein is precipitated by acetic acid, which will not account for the poor preservation of this material by glacial

acetic acid. The reaction of protalbumose is more nearly identical with the observed reactions. Protalbumose is precipitated by alcohol, but in a soluble form, according to Mann, accounting for the comparatively poor fixation with alcohol. Osmium and formaldehyde might be expected to fix protalbumose poorly according to Mann's table. The fact that protalbumose is soluble in high grades of acetic, but insoluble after treatment with the low grades also suggests that this may be the material found in the center of the endosomes. Like many other types of substances, protalbumoses are well preserved by chromic acid and sublimate. Artificial digestion experiments support this view. On the basis of the present information, the writer is inclined to the opinion that the inner endosomal substance is composed of protalbumose, or some closely allied substance, although much more work is necessary before any definite conclusion is possible.

Central ground-plasm.—The ground-plasm of the central region is transparent and structureless in living nuclei. Schubotz (1905) believed that he could see a fine reticulum in the central region of living nuclei, but in the material studied for this investigation, this was not observed. The central region, like the peripheral region, is essentially acidophilic in its reactions to stains, but in other respects it is distinctly different. It appears that the acidophilic reaction of the central ground-plasm reaches its height in the middle of the interphase period, and the substance becomes more basophilic as division approaches, although it never becomes intensely so.

Many amoebae do not react positively to the Feulgen test for nucleic acids. *E. blattae* has been thought to belong to this group. Morris (1936, p. 230) says, "Although tried in many variations the Feulgen reaction gave uniformly negative results, although ciliates on the same slides stained well." The results of this study do not confirm his results, except during the interphase of the trophic stage. Sassuchin (1936) also reports that the nucleus of *E. blattae* does not react with the Feulgen reagents, but suggests that at other parts of its life cycle, it may show a positive reaction. As Sassuchin suggested, the nucleus does not remain negative to the Feulgen reaction throughout the life cycle. Although invariably negative to the Feulgen reaction during the interphase, the central region gradually becomes somewhat diffusely positive during the early division stages, and the chromosomes which are formed from the substance of the central ground-plasm are distinctly positive. During the reorganization of the nucleus after division, the chromosomes break down, and the formation of a new central region from the chromosomal substance is accompanied by the gradual disappearance of the positive reaction with the Feulgen reagents. While the Feulgen reaction is quite

possibly not specific for nucleic acids, it is the best test which we have at present for them. The fact that after fixation with alcohol the nucleic acids are precipitated, but in a soluble condition, and that nuclei fixed in alcohol showed chromosomes which were poorly preserved and failed to react well with Feulgen reagents, although the techniques used were the same as those which gave good reactions during similar division stages after fixation in compound fixatives, supports the idea that the reacting substance was nucleic acid. The results of fixation of the chromosomes and the central region during stages just prior to or just after division in various simple fixatives shows that the Feulgen-positive substances and the chromosomes reacted as one would expect nucleic acid to react according to the table shown by Mann (1902) and the similar work of Fischer (1899). In view of these facts it is believed that the Feulgen-positive material in *E. blattae* is a thymo-nucleic acid, and that the nucleic acid content of the central region fluctuates during the division cycle, reaching a peak during the anaphase-like stage while the chromosomes are clumped at the poles of the dividing nucleus, and disappearing during the reconstruction of the nucleus. It appears probable that the disappearance of the nucleic acids involves a combination of the nucleic acid into a nuclein or nucleoprotein. During the interphase the substance composing the central ground-plasm appears to react, in general, similarly to nucleoproteins. It shows considerable resistance to digestion with pepsin-hydrochloric acid, and in other respects appears to show some similarities to nucleoproteins. Although it usually shows affinities for acid dyes, it seems probable that the central ground-plasm during the interphase stage is composed of a nucleoprotein, different, certainly from the one noticed in the endosomal cortex. It is most probable that the nucleoproteins of the central ground-plasm are associated with various other compounds, of which the majority appear to be of a protein nature.

Imbedded in the central ground-plasm are delicate granules in some nuclei. They are quite invisible in the living nucleus, but the regularity with which they appear in fixed nuclei in which diverse techniques have been used suggest that they are not artifacts. Schubotz (1905) observed such granules, and from artificial digestion experiments came to the conclusion that they were the only chromatin in the nucleus. This does not agree with the results of the present study with respect to artificial digestion experiments (see p. 32), and it is possible that Schubotz used different concentrations of hydrochloric acid or pepsin. Janicki (1909) also described chromatic central granules. Kudo (1926) states that the central region usually contained no chromatin granules except during early division stages, when he believed that the chromatin granules may migrate into the central region. In the material studied it seems probable that, as Kudo observed, the chromatin granules occur in the central

region only in stages approaching division and that the central region granules are peculiar to early kinetophase nuclei. No evidence in favor of the migration of peripheral granules into the central region could be found, however, and it seems probable that the granules are associated with the chromosomes, for when they first appear the chromosomes assume a beaded appearance. These granules are somewhat basophilic, but not distinctly so, and are not specifically positive to the Feulgen test. They appear to be equivalent to the granules described on the chromosomes of *E. disparata* by Kirby (1927). It is possible that these granules represent the collected nucleoprotein of the central region, but although early observations point to this inference, not enough work has been completed on nuclei in this stage to make a definite conclusion possible.

Hyaline body.—After Flemming or Champy fixation a hyaline structure may be found in the central region. It was found in fixed nuclei only, but Sassuchin (1930) reports having seen a body in the central region of living nuclei which he believes is identical with the "karyosome" of Janicki (1909). Similarly Bütschli (1878) reported that there was a dark body visible in the central region of some nuclei. Mercier (1910) and Kudo (1926) did not observe this structure in living or fixed nuclei, but Janicki (1909) gives a good description, although his figures are not very clear. According to Janicki it is homogeneous and lies at one pole of the central region. It is almost constant in position. It initiates karyokinesis by its division and the formation of a spindle from its substance. Although his description of its position and general appearance seems to fit the hyaline body, no relationship to division as reported by Janicki has been observed. He termed the structure a karyosome, but it seems that since it does not appear to be homologous structurally or functionally to the structure ordinarily called a karyosome in other amoebae, another term should be used.

In nuclei stained with safranin the hyaline body is most prominent. It is much more difficult to distinguish in haematoxylin preparations. It is less basophilic than the endosomes and its constant position at one pole of the central zone is so characteristic that it can usually be recognized easily. It is most evident during the late kinetophase and early interphase period, when it lies at the pole of the dedifferentiating chromosomes as a distinctly basophilic body. During later interphase development it is no longer basophilic, and finally disappears altogether. No spindle has been observed in the dividing nuclei, and a division of the hyaline body has never been witnessed. It first appears when the chromosomes are clumped at the poles of the nucleus, and at the present time its mode of formation is wholly unknown. It appears to be associated with the reorganization of the nucleus after division.

Concerning its reactions with simple fixatives, it is interesting to note

that it may possibly consist of a material closely allied to a protamine. Protamine is precipitated in an insoluble form by chromic acid and mercuric chloride, according to Mann (1902). It is not precipitated by acetic acid nor formaldehyde. It is precipitated in a difficultly soluble form by alcohol. The hyaline body is found after mercuric chloride fixation in prepared mounts. It is observed in cells immediately after fixation in alcohol, but not after washing for long periods of time. It is worthy of note that while protamines are insoluble in absolute alcohol, they are soluble in the lower grades. It was not observed after acetic acid fixation, nor after formaldehyde nor chromic acid. In osmium-fixed material it is incompletely preserved. The absence of the hyaline body in chromic acid material seems to deny that it is a protamine, but it may be pointed out that while it is incompletely preserved by osmium, it is well fixed by the osmic-chromic combination of Flemming's fluid. This may indicate that the chromic acid had some effect on the hyaline body during Flemming fixation.

It is interesting to observe in this connection that the hyaline bodies appear to be very closely associated with the chromosomes during the reconstruction of the central region after division. This is accompanied by a definite shift in the reaction of the substance composing the chromosomes in the staining reactions. Up to the time of the appearance of the hyaline body the chromosomes react positively to the Feulgen test. While it is present this positive reaction is lost, and when it disappears, the central region is composed of Feulgen-negative substance. That protamine has a strong affinity for nucleic acids has been known for a long time, as pointed out by Mann (1902). It is a characteristic substance in the sperm of lower animals, where it appears to be connected with the development of large amounts of nucleic acid found in the mature sperm. It is suggested by the above that the hyaline body may possibly have some similar functional importance in the nucleus of *E. blattae*, if it is indeed composed of a substance resembling protamine. It may be associated with the reduction in nucleic acid content of the chromosomes during their dedifferentiation. This may account for the shift in stainability of a hyaline body, as the nucleic acid from the chromosomes forms a basophilic compound with the substance composing the hyaline body.

XIII. NATURE OF THE CHROMATIN

THE EXACT definition of chromatin is somewhat uncertain at the present time. It has altered a great deal in its significance since the term was first coined to indicate the dark-staining material in the nucleus. It became increasingly apparent as the nuclear activities were more completely understood that the dark- and light-staining materials might be more

closely related functionally than was originally believed. The concept of oxychromatin and basichromatin, developed by Flemming, defined the dark-staining material as basichromatin because it stained with basic dyes, and the light-staining material oxychromatin because it stained with acid dyes. There was an attempt to distinguish between achromatin, the so-called "linin" or nuclear reticulum from the oxychromatin, but this was very indefinite, and, as stated by Sharp (1920, p. 64), "As used by many writers the term oxychromatin includes also the linin, so that in much of the cytological literature linin and oxychromatin are more or less interchangeable terms, while "chromatin" refers to the basichromatin."

Bělař (1926) summed up some of the objections to the older conception of chromatic elements in the nucleus. He found the term "achromatin," as distinguished from oxychromatin, undesirable. He says (p. 243), "Es erscheint daher immer nach vorderhand zweckmässiger, solche 'achromatischer' Strukturen, denen vitale Realität nicht aberkannt werden darf, einfach als Differenzierung der amorphen Kerngrundsubstanz zu bezeichnen." He expresses the opinion that the term chromatin is a functional rather than a chemical one. Thus he says (p. 243), "In denjenigen—noch dazu recht seltenen—Fällen, wo an chromatischen Strukturelementen, deren vitale präexistenz feststeht, eine Unterscheidung von acidophiler und basophiler Substanz möglich erscheint (z. B. die sogenannten Chromomeren und das chromatische Chromosomen 'skelett'), sei jedoch daran erinnert, dass der chromatin begriff letzten Endes ein *morphologischer* ist und dass wir nicht selten aus neutral oder gar acidophil reagierenden Strukturen Chromosomen hervorgehen sehen." Following this line of thought the chromatin cannot be analyzed chemically, since (p. 241), "Eben diese morphogenetische Analyse zwingt uns aber andererseits, in vielen Fällen Strukturen, die sich färberisch entgegengesetzt oder neutral verhalten, ebenfalls als Chromatin zu bezeichnen, sobald nämlich der Nachweis erbracht ist, dass sie genetisch mit den Chromosomen zusammenhängen. Die Ausdrucksweise 'chromatinarmer' und 'chromatinreicher' Kern is somit als Unfug zu bezeichnen." Thus Bělař's concept appears to have diverged far from the classical basichromatin-oxychromatin concept.

Gutherz (1927) differs in his interpretation of chromatin. He says (p. 332), "Im folgenden wird 'Chromatin' ausschliesslich zur Bezeichnung basophiler, d. h. mit basischen Färbstoffen elektiv färbbarer Substanzen innerhalb des Zellkernes bzw. in den ausgebildeten Chromosomen verwendet werden. . . . Der Begriff 'Oxychromatin' scheidet definitionsgemäss für unsere Betrachtung aus." He, thus, disposes of the term oxychromatin by considering only basophilic material as chromatic.

Sharp (1934) refers the question of the nature of the difference

between basic and acidophilic materials in the nucleus to either a physical difference, a chemical difference, or a combination of the two. He says (p. 55), "It has been suggested that if there are two elements, chromatin and linin, they are not so distinct morphologically as the earlier workers supposed, the chromatin existing rather as a thin fluid impregnating the linin substratum. The chromatic lumps are often not sharply set off from the rest of the thread but taper off gradually. In such cases it has been found that purposes of cytological description are well served by the conception of a reticulum composed of a single complex substance which stains variously in different regions and at different stages of the nuclear cycle, according to the size of the strands, their physico-chemical state, and the technical procedure employed. This one substance is loosely spoken of as chromatin, but because of the long application of this term to a supposedly distinct component of the reticulum it is advisable to use Lundegardh's (1910) term *karyotin* for the reticular substance as a whole. Only future research can decide whether karyotin ('chromatin' in the wide sense) is a true chemical compound or a looser combination of two or more constituents, only one of which is 'chromatin' (in the narrow sense)."

In the present study, it would have been possible to term chromatin, following Guthertz's basophilic concept, to apply to the endosomes and peripheral granules only, except for the very light basophilic reaction of the chromosomes, which might be included as chromatin-containing structures. By using Bělař's functional definition, the comparatively non-basophilic material of the central region would be termed chromatin, since it is from this substance that the chromosomes are formed. The broad sense suggested by Sharp would lead to the whole nuclear contents, except, perhaps, the peripheral spherules, to be considered as chromatin. Of course, not all of the points of view expressed about chromatin have been cited, and still other interpretations might be made, based on other uncited and unmentioned opinions. This great confusion makes it quite difficult to use the term chromatin until some future studies and discussions have unified the concept.

The variety of nuclear elements in this organism makes it doubly difficult to reach a definition of chromatin. It was decided that some attempt to study the nucleus with the so-called specific chromatin tests might lead to a possible solution. In this attempt to determine the relation of chromatin and the various nuclear elements the following tests were applied: the Feulgen nucleal reaction, acidified methyl green, 10 per cent NaCl solution, comparison of the action of 10 per cent KCl and CaCl₂ with the NaCl solution, and artificial digestion experiments.

The development of a technique by Feulgen and Rossenbeck (1924)

which could be applied to cytological material for the demonstration of free nucleic acid made it possible to determine the distribution and relationship of nucleic acid to the nuclear elements. It has been pointed out by numerous investigators that the Feulgen nuclear reaction is not to be considered as specific for nucleic acids. There is the substance plasmogen, in the cytoplasm, which gives a positive reaction, unless removed by solution in 95 per cent alcohol, and in addition there are other compounds which may occur in the cytoplasm of various types of cells which will react positively. In spite of all these various objections the Feulgen nuclear reaction is the best that we have at the present time, and the writer is of the opinion that for substances within the nuclear membrane it is most advantageous to consider it specific for nucleic acids until further microchemical tests have made it possible to refine our present concept. For that reason, and with these reservations, the writer has used the terms nucleic acid, and Feulgen-positive material interchangeably. Only substances within the nucleus are considered here, and the positive reaction in the cytoplasm is not referred to. By comparing the intensity of the reaction of the nuclear substances with the Feulgen reagents as indicated by a deeper violet color, it was possible to estimate comparative amounts of nucleic acid present at different periods. The writer wishes to point out that although this is distinctly a qualitative test, it may yield a rough quantitative measure of a substance or group of substances which, for lack of a more accurate term, have been called nucleic acids, not in the strict chemical sense, but in a loose cytological sense. Observations of the effects of the nuclear reaction at various times during the trophic phase of the life cycle have revealed a distinct cyclical variation in the amount of nucleic acid present in the nucleus of *E. blattae*, associated with the division cycle.

During the middle and late interphase periods there is no reaction demonstrable in the nucleus of *E. blattae*. Because of the comparatively short time required for the nucleus to complete its division, this includes well over 95 per cent of all the nuclei seen in the present study. At this time the whole nucleus, following the standardized Feulgen technique cited previously, gives no reaction which is visible with the Feulgen reagents. The nucleus stains with the acid dyes. As the kinetophase approaches, however, the central region of the nucleus begins to show a very light violet reaction. This was so weak that it was not noticed in the first preparations, and it was not until later stages were studied in which a more decided reaction was obtained that the earlier stages were found to be positive. As the kinetophase advances the original diffuse reaction becomes more intense and the anlage of the chromosomes appear. At this time the chromosomal strands do not appear to be positive to a greater

degree than the surrounding material. Granules appear in the central region at this time, and the chromosomal strands, the granules, and the ground-plasm are all positive to approximately the same degree. Following the so-called "dedifferentiated" stage of nuclear division, when a reorganization of the peripheral material is completed, the amount of nucleic acid present as indicated by an increased deepening of the Feulgen reaction increases quite rapidly. As the chromosomes migrate to the poles of the nucleus they enter a massive condition in which the granules cannot be distinguished readily in most nuclei. At this time they are colored most intensely by the reaction. Even at this time they are by no means dark, and, as compared to the macronucleus of the ciliates *Nyc-totherus ovalis* and *Balantidium praenucleatum* which occur on the same slides, the coloration would be termed quite light.

Until the chromosomes begin to dedifferentiate the Feulgen reaction continues to be comparatively intense. As soon as the chromosomes begin to fuse together and form the new central region of the daughter nucleus, the amount of nucleic acid present appears to decrease rapidly. At this time the hyaline body, lying very closely pressed against the clumped chromosomes, occasionally shows a very light positive reaction. This, however, is not sufficiently regular to permit considering it a normal part of the division cycle. It does, however, normally present a somewhat basophilic aspect at this time. As the chromosomes alter their shape, and finally form a new central region, the violet color disappears entirely. After the endosomes have attained the sinuous strand stage (Fig. 1), the central region no longer reacts positively to the Feulgen test.

In two nuclei of the thousands observed the endosomal material was colored a very light violet shade by the Feulgen reaction. Both of these nuclei were fixed in Gilson-Carnoy. This appears, from its extreme rarity, to be an atypical condition, for in no other case was a positive reaction with endosomal material observed. It is possible, of course, that there is a minimal reaction so slight that it cannot be seen, but with the present development of the Feulgen technique, the endosomes must be considered as negative to the test.

Taken as a specific test for chromatin, the nucleus appears to be wholly lacking in chromatin at times, and never liberally supplied with it. Of course, as with the endosomes, it is possible that there is a subminimal reaction which is not visible, but until further tests are possible this must remain a somewhat dubious possibility. Whatever chromatin normally occurs in the nucleus appears to be present in the central region in normal nuclei. This material, it may be pointed out, is identical with the material which forms the chromosomes, and more or less closely parallels the interpretation of chromatin advanced by Bělař (1926), in-

sofar as division stages themselves are concerned. The long interphase condition would be a period in which the chromosomal material would not be chromatic, however, if the Feulgen test be considered specific for chromatin.

Although approaching a test for chromatin as defined by Bělař, the Feulgen reaction fails utterly as a chromatin test if any other definition than Bělař's be accepted. It does not react with the peripheral basophilic elements, and thus falls short of demonstrating the supposed chromatic elements if any connection between affinity for basic dyes and chromatin be postulated.

To some extent the Feulgen reaction might be considered as specific for the "chromatin in the strict sense" mentioned by Sharp (1934), and would fail absolutely to demonstrate the "chromatin in the wide sense." It fails to demonstrate the former in the interphase state, however, and thus stands in the same relation to Sharp's "chromatin in the strict sense" as it does to Bělař's chromatin determined by its relation to the chromosomes.

As a result of this, the conclusion must be reached that chromatin is not demonstrated specifically by Feulgen's nucleal reaction. Regardless of its value or lack of value as a specific test for nucleic acids, it is not sufficient in itself to determine the chromatic elements of the nucleus, insofar as *E. blattae* is concerned, unless we are willing to admit that during the interphase condition *E. blattae* is lacking enough chromatin to give a positive reaction.

Methyl green has been known as a specific test for chromatin for a long time. It is used as a temporary stain, applied directly to the living organism in a solution acidified with 1 per cent acetic acid. The 1 per cent solution of the dye, which has been widely recommended was found to be too strong for *E. blattae*, and a 0.25 per cent was found to be much more efficacious. The same technique was used for the study of the effects of methyl green as were used for the observation of the immediate effects of fixation.

As the acidified methyl green struck the organism death occurred instantaneously. It was accompanied by a slight swelling of the nucleus. The membrane was more sharply outlined after fixation, and appeared to be somewhat thinner than in life. It acquired a very light green tint. The peripheral ground-plasm was also tinted a light green color at first, but this gradually changed to a violet color, during the first eleven minutes or so, due to the metachromatic effect of the methyl violet present as an impurity in the stain. The peripheral granules became very slightly more prominent during fixation, and were stained a somewhat darker green than the peripheral ground-plasm. The endosomes became more promi-

nent after fixation and were stained a rather dark green. They were approximately as dark as the most intensely stained peripheral granules (Fig. 35). Sometimes in the larger endosomes the cortical and medullar parts of the endosomes could be identified. The central region was not very clear, but appeared to be stained a very light green, approximately the same as the peripheral ground-plasm and the cytoplasm.

Using methyl green as an indicator of chromatic material the chromatin would appear to be centered in the peripheral granules and the endosomes. This coincides with the basophilic material, and would thus be specific for chromatin as interpreted by Gutherz (1927). In spite of this correlation of the methyl green test and the basophilic material, the writer feels that methyl green cannot be accepted as a specific chromatin test in *E. blattae*. Methyl green, being a basic stain, might be expected to demonstrate the basophilic elements of the nucleus, and can be considered no more specific than is haematoxylin, and possibly less so, since the differentiation between the stained and unstained parts of the amoeba are much less obvious. An obvious difficulty is that if we accept the basophilic definition of chromatin we are led to believe that the central region, which forms the chromosomes, are achromatic in the interphase, and contain very little chromatin during division, a condition which would hardly be anticipated from our concept of the close relationship of chromatin and hereditary units as observed in Metazoa. For that reason the writer feels justified in considering the acidified methyl green and other basic dyes as not demonstrating all of the chromatin in the nucleus and therefore not a specific chromatin test.

Zacharias (1881) found that chromatin was swollen, and finally dissolved by a 10 per cent solution of sodium chloride. This method has been used occasionally as a specific chromatin test. It was applied, using the same method as that employed for the study of the immediate effects of fixation, except that because of the greatly increased density of the organism resulting from the dehydration caused by the high concentration of the salt, it was necessary to compress the animal more than was necessary for the study of fixatives.

Except for a slight darkening of all of the components, the nucleus seemed unchanged when the solution was first added. There was a slight swelling of the whole nucleus, but no apparent focus of increase in size. The most careful attempts failed invariably to reveal a swelling of any single component. A few moments after the solution of NaCl was added there was a slight Brownian movement of the peripheral spherules. This continued to a slight degree throughout the remainder of the experiment. The nuclear contents had contracted away from the membrane slightly within three or four minutes. At this time the central region was probably

at least partially dissolved, for it was very clear, and in some cases there were a few peripheral spherules moving into it. The peripheral ground-plasm also went into solution partially, leaving the peripheral spherules and granules visible. The peripheral granules were the first to go into solution, after which the spherules gradually disappeared. It required from 15 to 20 minutes for the peripheral spherules to disappear entirely. After the spherules had disappeared a number of extremely delicate strands were revealed. These had been obscured by the spherules and remained invisible until the spherules were almost completely gone. They were very thin, just within the limits of visibility. These strands were not dissolved in 30 minutes, and later experiments, not involving constant observation, indicated that they were present even after longer periods.

These strands seem to represent the "achromatin" of the nucleus. The possibility that these strands represent the base on which the reticulum is formed cannot be entirely discounted, but the fact that they cannot be seen in the living nucleus makes it impossible at the present time to determine what their nature is. It is possible that they were formed as a result of the treatment with sodium chloride, and represent artifacts. Their minute dimensions and the fact that they are obscured in the experimental nuclei until the spherules are almost completely dissolved make it uncertain whether they could be seen in the living nucleus if present.

The solubility of the components would suggest that all of the remainder of the material is chromatic in nature if solubility in 10 per cent NaCl be considered a test for chromatin. This interpretation would differ widely from the more specific tests, which isolate one or another structure from the remaining nuclear parts. At the present time the writer is inclined to believe that the method used here cannot be utilized as a specific chromatin test, but might possibly be developed as a test for the "chromatin in a wide sense" as used by Sharp (1934). It seems almost impossible at the present time to speculate on the nature of the strands demonstrated by this technique. One obvious possibility is that they may represent the "linin" of the nucleus. In this case solution with 10 per cent NaCl might be developed in *E. blattae* as a means of separating the "karyotin" from the "linin."

Organisms were also exposed to solutions of 10 per cent KCl and CaCl₂ using the same methods. With the potassium solution the results were identical with those obtained with solutions of NaCl (Figs. 40, 41). The same structures were dissolved and fine strands were left in the nucleus at the end of the experiment. The potassium chloride appeared to react a little more rapidly than the sodium chloride, the whole process being completed in about 10 minutes.

Calcium chloride was not at all similar in its effects. As the solution struck the organism the nucleus underwent a great deal of shrinkage, accompanied by a great wrinkling of the membrane and indentation of the nucleus. The nuclear membrane disappeared rather rapidly, and the various components became less refractive. The peripheral spherules became quite indistinct. The central region disappeared when the indentation of the nucleus occurred, appearing to be crowded out of the picture. Addition of water caused the nucleus to swell, but when an indentation had formed, as was usually the case, it remained present. The peripheral spherules were found to be somewhat indistinct and were apparently partially fused. Prolonged action of the original calcium chloride solution did not bring about their solution nor otherwise alter their appearance.

It was concluded from this that the potassium chloride solution was as good for dissolving material from the nucleus as the sodium chloride in solutions of the same percentage. Whether either of them can be considered as specific tests for chromatin in *E. blattae* is extremely dubious, and is contraindicated by most of the modern conceptions of chromatin. On one point it seemed that results of some importance were obtained. In spite of the fact that the peripheral ground-plasm reacts to stains and fixatives in much the same way as the cytoplasm does, and is apparently basically a protein colloid, possibly containing other compounds in it, it reacts very differently than the cytoplasm to the sodium and potassium chloride solutions. This seems to indicate rather forcibly that the cytoplasmic and nuclear proteins are not identical in either physical or chemical states, or both. It was also concluded that calcium chloride could not be used as a nuclear solvent, and did not act in any way that was comparable to the action of sodium and potassium chlorides.

Resistance to digestion with pepsin-hydrochloric acid solutions has been used for many years as a test for chromatin. Schubotz (1905) is the only previous investigator to report the action of this solution on the nucleus of *E. blattae*. His results indicated that the chromatin occurring in the nucleus was restricted to small granules which gathered in the center of the nucleus. The results of the digestion carried on in this study differ somewhat from those reported by Schubotz. A 2 per cent solution of pepsin in 0.5 per cent hydrochloric acid was used at 37° C. By using a warm stage it was possible to keep the experimental amoebae under observation continually.

As the pepsin-hydrochloric acid came in contact with the organism, death was instantaneous. The cytoplasm became much darker and the nucleus was swollen. The nuclear membrane almost disappeared. The peripheral spherules were very rapidly dissolved, as were the peripheral

granules. The peripheral ground-plasm disappeared, in from 15 to 20 minutes, leaving only the endosomes and the central zone in the nucleus.

The endosomes became more prominent as the solution first came in contact with the organism. They were more refractive and homogeneous at first. Shortly after this first effect was consummated the endosomes began to alter in appearance. In the center of the endosomes a small refractive granule appeared, while a less refractive area surrounded it. The cortex of the endosomes, like the granule in the center, remained highly refractive. This endosomal structure, coinciding with the structure observed in fixed nuclei, seemed to indicate the early solution of the more lightly-staining inner substance of the endosomes, and a greater resistance of the basophilic outer material. After the inner structure became apparent the endosomes changed but little in the next hour. About an hour and a half after the pepsin-hydrochloric acid was first applied the endosomes showed signs of further dissolution. A distinct increase in the size of the vacuoles was noticed and there was a loss in refractivity of the whole structure. Partial fusion of the endosomes was a further indication that they were beginning to go into solution. By about three hours after the application of the pepsin-hydrochloric acid solution the endosomes were dissolved.

The central region was the most resistant to the digestion experiments. No alteration in the appearance of the central region had occurred in two hours except that the material composing it was precipitated and much darker than in the living nucleus. This change had occurred when the solution first struck the organism, and seemed to be an effect of the acid rather than of the pepsin. After three hours slight indications of disintegration had appeared, but these were very limited in extent.

Accepting the resistance to digestion as an indication of chromatic nature, the central region is the most chromatic region of the nucleus. The cortex and the dark-staining central granule of the endosomes represent the remainder of the chromatin. The endosomes, since they dissolve more rapidly than the central region, seem to be less chromatic than the central region. One of the most interesting points was the rapid solution of the basophilic peripheral granules. This may have been due to their small size as compared to the endosomes, or may possibly indicate a distinct chemical difference in the composition of the granules and endosomes. The writer is inclined to favor the latter interpretation, since the granule lying in the center of the endosomes was of about the same size as the peripheral granules, and persisted for several hours.

It is evident from this that the pepsin-hydrochloric acid digestion does not follow any staining reaction in its effect on the nucleus of *E. blattae*. It indicates a chromatic nature for the basophilic cortex of the

endosomes and a non-chromatic nature for the basophilic peripheral granules. It indicates the chromatic nature of the central region and the non-chromatic nature of the peripheral ground-plasm, both of which are more or less acidophilic in their staining reactions. In this respect it fails to follow precisely the definition of chromatin as presented by any of the previous writers with which the author is acquainted, and as such might be considered as non-specific for chromatin in the accepted sense of the term, whatever that may be.

For aid in comparison of the effects of the various tests that were attempted, a summary of the results may be gathered as follows:

Nuclear membrane.—Invariably negative to all tests, except that it stains with basic dyes after osmium fixation.

Peripheral ground-plasm.—Negative to Feulgen; usually unstained by basic dyes; negative to methyl green; dissolved by 10 per cent sodium and potassium chloride, but revealing a number of delicate strands of material resistant to the action of the solutions; dissolved by artificial digestion very rapidly. Thus the ground-plasm is achromatic in all tests except those with sodium and potassium chlorides, in which it appears to be composed of chromatic and achromatic parts, the latter being represented by a number of delicate strands.

Peripheral spherules.—Negative to Feulgen; usually resistant to all stains, except, perhaps, safranin after osmic fixation; dissolve in acidified methyl green; dissolve in 10 per cent sodium and potassium chlorides; dissolve in pepsin-hydrochloric acid. The spherules are therefore negative to all tests except solution in sodium and potassium chloride, in which they give a positive reaction to the chromatin test.

Peripheral granules.—Negative to Feulgen; stained by basic dyes; stained by acidified methyl green; dissolved by 10 per cent sodium and potassium chlorides; dissolved by pepsin-hydrochloric acid. These are inconsistent, being negative to Feulgen and artificial digestion experiment, but positive to the others.

Endosomes, cortical layer, and central granule.—Negative to Feulgen; positive to all other reactions. They are digestible in pepsin-hydrochloric acid, but very slowly so.

Endosomes, inner vacuoles.—Negative to all tests but solubility in 10 per cent sodium and potassium chlorides, in which they apparently dissolve, and to basic dyes, with which they show a slight reaction.

Central ground-plasm.—Negative to Feulgen, except immediately before and immediately after division; usually negative to basic dyes, but always more basophilic than the cytoplasm; unstained by acidified methyl green; soluble in 10 per cent solutions of sodium and potassium chlorides;

resistant to artificial digestion. The alteration in nucleic acid content as measured by the Feulgen reaction makes it periodically positive and negative to that test. Otherwise the central region is uniformly positive for chromatin. The poor stainability of the central ground-plasm to basic dyes as compared to the endosomes is offset to some extent by the fact that it is somewhat more basophilic than the cytoplasm.

The diversity of the results need not be pointed out. As mentioned above, there are difficulties in accepting any of the above as a specific chromatin test, and the choice of any seems to be left up to the discretion of the individual. Since arbitrarily accepting the Feulgen reaction as a specific chromatin test involves the contention that for the greater part of the interphase period the nucleus is composed entirely of achromatic material, or contains subminimal amounts of chromatin, it seems untenable. That nucleic acid is released from nucleoprotein or some similar material at the time of division appears to be quite probable in the case of *E. blattae*. That this same nucleic acid is recombined into more complex nucleoproteins or similar substances is an almost inseparable corollary, to account for the disappearance of the Feulgen-positive material after division. The close relationship of nucleic acid and nucleoprotein when considered from a morphological and functional point of view make it undesirable to differentiate between them, calling one chromatin and the other achromatin. Such functional inconsistencies may be expected from any concept of chromatin as a static chemical compound.

Similarly it seems undesirable to interpret all of the basophilic as chromatin and none of the acidophilic material as chromatin. The technique employed in preparing a slide is often very important in determining what will be basophilic and what acidophilic in reaction. In this respect the fixative is of greatest importance. For example, it is quite improbable that the nuclear membrane is chromatic, and yet it reacts as a basophilic structure after osmic fixation. Furthermore the acceptance of the basophilic point of view would require the belief that the chromosomes and the material from which they arise during division is largely non-chromatic, and that the endosomes, having no relationship to genetic factors insofar as can be found by analogy with other cytological observations are the most chromatic elements of the nucleus.

Bělař's point of view avoids some of the more obvious difficulties. By identifying the chromatin as those materials which are genetically associated with the chromosomes, he develops a functional point of view which makes the actual chemical nature of the material unimportant. To a great extent, this is an interpretation which eliminates all of the objections of the tests mentioned above. If in some organisms, like *E. blattae*, and some of the other Protozoa, as mentioned by Sassuchin

(1936) which show a positive reaction to the Feulgen test at restricted points in their life cycle, there is a chemical change in the material associated with the chromosomes, Bělař's concept of chromatin will include them readily enough.

On one point, however, the interpretation of chromatin as stated by Bělař fails to wholly satisfy the conditions observed in *E. blattae*. It seems logical that if the term chromatin is to have a functional significance as he suggested, it should include not only that material which is most active during the division of the nucleus in distributing genetic factors, but that the active material of the interphase period should also be included. Since the mere distribution of genetic factors is unimportant unless they do function during the interphase condition, the functional interpretation should include the structures which appear to undergo the greatest activity during the interphase. In most nuclei there is no morphogenetic difference between the structures which are derived from the chromosomes and the structures functioning during the metabolic activities of the nucleus in interphase, insofar as we are aware at the present time. In *E. blattae*, however, activity in the interphase appears to center in the endosomes, which, insofar as can be determined, are not derived from the chromosomes at each division and receive no material from the chromosomes during interphase. This leads to the point of view that the endosomes, as well as the central region material associated with the chromosomes, should be considered as chromatic. Since the inner light-staining material seems to be developed during the interphase period, and since it is possibly developed from the outer basophilic portion of the endosomes, the basophilic material is believed to be the active part of the endosomes.

The results of the study of the possible chemical composition of the nuclear elements show that the endosomal material and the chromosomal material are the only elements which appear to be composed of nucleic acid or nucleoprotein at the present time. This functional point of view as outlined above does not diverge an excessive amount from a chemical view, although it seems quite true that the nucleoproteins composing the central region and the endosomes, from their staining reactions, are probably chemically different, or, at least, in a different physical state.

The closest approximation to a specific chromatin test, if the above point of view be maintained, was obtained with the pepsin-hydrochloric acid. Realizing that future work may greatly alter our present concepts, it is impossible to offer any static and final concept, but, with the present information, it seems possible to infer that pepsin-hydrochloric acid digestion does isolate and differentiate between the chromatic and non-chromatic material of the nucleus, and, further, offers an opportunity

to differentiate between the morphological structures which appear to be most active in the interphase and in the dividing stages of the nucleus, at least for *E. blattae*.

XIV. THE PRECYSTIC PERIOD

THE PRECYSTIC organisms may be distinguished from the trophic organisms by their smaller size, their clearer cytoplasm, and the presence of two or more nuclei. They are typically quite active until just before the formation of the cyst wall, when they become quiescent and round up into a spherical shape.

Bütschli (1878) was the first to describe the precystic amoebae. He noticed that in addition to large uninucleate individuals there were a number of smaller organisms with several nuclei. Nuclear size was inversely proportional to the number of nuclei, and the organisms with more nuclei were usually somewhat smaller. The ones with many nuclei were frequently quiescent and rounded in shape. Nuclei were typically spherical, but sometimes were irregularly elongated or spindle-shaped. The appearance of the nucleus differed from that of the larger forms in that the interior was a large fluid-filled cavity, and nuclear contents were restricted to a narrow band at the edge of the nucleus in contact with the nuclear membrane. Bütschli's observations were made on living amoebae.

Schubotz (1905) saw amoebae with up to 20 nuclei. They were regularly smaller than the trophic forms, and he believed them to be precystic. In the multinucleate amoebae the nuclear membrane was much thinner, appearing as a single line instead of a double-contoured structure. In the living condition they were quite similar to the nuclei of the trophic stages, except that there was a smaller number of peripheral granules and nucleoli.

Elmassian (1909) described the formation of two kinds of cysts. He termed these dark and light cysts. The precystic stage of the dark cyst was an amoeba with a single large typical nucleus, with endosomes. It was indistinguishable from the trophic amoeba, except for its clearer cytoplasm and somewhat smaller size. As the organisms secreted a gelatinous coat the nucleus exploded, releasing secondary nuclei, which developed into the cyst nuclei. The light cysts were developed from amoebae containing a single large nucleus which had undergone a morphological transformation involving the total destruction of the endosomes and the formation of a large number of tiny chromatic granules. The nucleus divided and a gelatinous cyst wall was formed, which ended the precystic development.

Mercier (1910) believed that the first step towards encystment was

extrusion of chromatin from the trophic nucleus, after which the nucleus divided. The peripheral and central zones of the two nuclei resulting from this division were poorly defined. During the division of these nuclei a centrosome occurred at each pole, and extending between them was an achromatic spindle. The chromatin occurring on the spindle was in the form of small spherical chromosomes. These divisions were not always synchronous, resulting in the production of amoebae with 3, 4, 5, 6, 7, or 8 nuclei. In the interphase the central region contained an area of achromatic ground-plasm in which large chromatic chromosomes and small achromatic granules could be found. The peripheral zone was finely granular. Nuclear division was initiated by division of a small granule found in the central region, which he termed the centrosome. The finely granular central zone divided, and a spindle extending from pole to pole was formed. The chromosomes became arranged on the spindle and moved to the two poles. The number of chromosomes was not determined in dividing forms, but appeared to be about 8 in the interphase nucleus. At the time of the formation of the cyst wall the nuclei were invariably clumped at the center of the cyst. This occurred when there were 8 nuclei in the amoeba in most cases.

Although Kudo (1926) did not study the precystic stage specifically he described an interesting migration of nuclei in an amoeba apparently preparing to encyst. There were 4 nuclei which moved to the periphery, and at one time a superficial resemblance to budding resulted. Later they were drawn back into the cytoplasm, however.

Morris (1936) found that precystic amoebae were characterized by nuclei which had a reduced amount of peripheral chromatin. The "karyosome" or central granule lying in the central region was much easier to observe in the precystic stage. Nuclear division of a type essentially like that of the trophic nucleus continued until 8 or 16 nuclei were formed. After these divisions a reorganization of the nucleus occurred during which the nuclear wall was reduced in thickness and the chromatin was arranged along the nuclear wall at regular intervals. A number of achromatic radii connected the central region to the nuclear wall. After the nuclear transformation the amoebae rounded up and the nuclei migrated to the center of the body, where they were arranged in a compact clump during the formation of the cyst wall.

XV. THE TRANSFORMATION FROM TROPHIC TO PRECYSTIC PERIOD

THE CYCLE of an infection with *E. blattae* is but little known. Cleveland and Saunders (1930) found that infections with *E. histolytica* follow a regular course, involving a gradually accelerated division rate inversely

proportional to a gradual decrease in the size of the amoebae. Morris (1936, p. 234) remarks concerning *E. blattae*, "Where numbers in infections are comparatively small, the individuals are habitually larger and show fewer indications of recent fission, while the approach of encystment is uniformly accompanied by increasing numbers of smaller animals which are usually in some stage of division or show signs of recent completion of this process."

Several questions are raised by a consideration of these statements. Are the trophic amoebae smaller in heavy infections, and if so, do they show signs of a more rapid division rate? Is a high division rate always accompanied by smaller size and encystment, or is it associated with the density of population? Are cysts produced only in heavily infected cockroaches, and if not, does the division rate increase in amoebae approaching encystment?

Cyst production was observed in both light and heavy infections. In either case, the amoebae which, as shown by their smaller size and less abundant food vacuoles, were approaching the precystic condition showed a definite increase in division rate. This increase in frequency of division was apparently independent of the density of the amoebae population of the host. A larger number of precystic individuals were found in the more heavily infected cockroaches, but not necessarily a higher percentage of precystic individuals. The indications of a higher division rate in the trophic forms in heavily infected hosts were not very clearly expressed, and the large trophic forms of heavily and lightly infected hosts appeared to average about the same size. It becomes rather clearly indicated by these points that the rapid divisions leading to the formation of cysts are independent of population factors in the case of *E. blattae*, at least in some cases, but that the transformation from the trophic to the precystic condition is accompanied by a definite increase in division rate independent of the population density. The increase in division rate leads to a change in the nuclear appearance, which makes it possible to recognize which are developing toward the precystic condition.

The early stages of the transition cannot be followed, for the series of rapid divisions which end in the precystic stage are not unlike those of the trophic part of the life cycle. As the cytoplasm becomes less filled with food vacuoles, however, the amoebae begin to decrease in size as a result of the divisions and lack of food and can be distinguished with comparative ease. The nucleus is smaller and the nuclear membrane is thinner, although still heavy enough to form a double-contoured image under oil immersion. The division of these nuclei is still typical until the late kinetophase is reached. When the chromosomes are clumped at the poles of the daughter nuclei the segregation of the peripheral and chromosomal material is very distinct. The chromosomes do not undergo

the rapid clumping which occurs in the division of the trophic individual, and the migration of the peripheral material around the chromosomal mass is delayed (Figs. 59, 60, 61). The segregation of the two nuclear regions is maintained for a longer time, and the chromosomes often form a loose reticulum instead of massing together (Fig. 62). The reticulum formed by the peripheral and endosomal material is much more slow to migrate around the central region and is noticeably smaller in amount in these stages. By the time that several such divisions occur the amount of endosomal and peripheral material is greatly reduced. Interphase reorganization is rather restricted, as the next division begins very soon after the last is completed. These interphase nuclei are characterized by the much smaller proportion of endosomal and peripheral material to central region than is the case with the trophic amoebae. This appears to result from the failure of the nucleus to form new endosomal material and new peripheral ground-plasm as rapidly as the nuclei divide. Since there is some evidence that this synthesis of peripheral material occurs at least partially in the interphase, the shortening of the interphase period is believed to be a possible factor in bringing about this reduction. The restricted amount of food may be another indirectly operating factor.

Living amoebae during this period are characterized by the more dense and clearer cytoplasm. The food material is reduced in amount and there are few or no food vacuoles. They are extremely active, however, undergoing locomotion which, size considered, is much more rapid than is the case of the trophic amoebae. The nucleus is smaller and the peripheral spherules fewer in number. The endosomal material is often more prominent as a result of the reduction in the peripheral spherules. The central region occupies a relatively larger proportion of the nucleus.

Fixed nuclei are characterized by a thin acidophilic membrane within which lies a narrow band of acidophilic peripheral ground-plasm bearing peripheral granules and endosomal spherules staining deeply with haematoxylin and safranin but negative to the Feulgen test. The granules are relatively few in number. The endosomal material is in the form of small spherules, which are smaller in size, although they lose none of their affinity for basic dyes. They no longer appear to be composed of a basophilic shell and a less basophilic core. The central region is usually acidophilic in its reactions to haematoxylin and, to a smaller extent, to safranin. A basophilic centriole may occasionally be demonstrated. In Flemming-safranin preparations the hyaline body is more prominent than in the trophic nucleus. Its division during the early kinetophase, as described by Janicki (1909), has not been observed, although it can be found in comparatively later stages of nuclear reorganization following division than is the case in the ordinary trophic

amoebae. The kinetophase begins when the central region appears to increase in its affinity for basic dyes. The chromosomal material moves away from the nuclear membrane and forms a coarsely reticular, dedifferentiated stage, which is followed by the arrangement of the peripheral spherules and peripheral granules in rows between the poles of the elongating nucleus. The chromosomes migrate to the two poles, without apparently undergoing a metaphase stage, where they form a rosette of strands, which often may be replaced by a loose reticulum of tangled chromosomal strands. The endosomal spherules become arranged on the reticulum formed by the peripheral ground-plasm in the median part of the nucleus, and shortly thereafter the nucleus begins to constrict. In the daughter nuclei which are formed, the isolation of the peripheral and central zone material is more complete than in trophic individuals. As the hyaline body appears at the poles of the daughter nuclei associated with the chromosomal mass, the definitive central zone is formed. The amount of peripheral material is reduced to a small vestige remaining at the pole opposite the chromosomes. The hyaline body becomes somewhat more resistant at this time and may be located after fixations which destroy it in the normal trophic individuals. Glacial acetic acid will preserve the hyaline body of such amoebae, approaching the precystic condition. It appears to be distinctly more basophilic at this time than is the case in the trophic nucleus.

XVI. THE LIVING PRECYSTIC AMOEBIA

THE PRECYSTIC stage begins when a suppression of cytoplasmic division after nuclear division brings about a binucleate condition. Nuclear divisions continue until between 8 and 16 nuclei are present, when a nuclear transformation occurs. Following the nuclear transformation a period occurs during which there is active locomotion, but no food is engulfed and no visible alterations in the nuclei occur. This appears to be a comparatively long period, as pointed out by Morris (1936). The rounding up of the organism is followed by the formation of the cyst wall. Nuclear changes accompany the formation of the cyst.

The early precystic period, extending from the binucleate stage to nuclear transformation, involves several nuclear divisions which have not been observed in life. The active amoebae are about 25 to 35 μ in largest diameter. Few food vacuoles are present, and these are almost invariably incompletely digested. The cytoplasm appears to be somewhat more dense than in the trophic amoebae, but this density is not accompanied by any decrease in activity, for the organisms are always actively motile. They usually move in a "limax" form, with but one broad pseudopodium

being formed. Cytoplasmic striation during locomotion is not infrequent. Cytoplasmic inclusions have been studied in some individuals in permanent mounts and with vital dyes. Mitochondria apparently do not undergo any significant alteration. The neutral red-stainable inclusions are present. The granules are present in large numbers (Fig. 74), but the larger spherules are greatly reduced in number. In many precystic amoebae the spherical inclusions are entirely lacking. The granules are osmiophilic, as in the trophic amoebae.

The nuclei are variable in number. They are usually rather small, the size being reduced as the number of nuclei increase. The nuclear membrane is relatively thin, and the transparent central region is relatively much larger than in the trophic amoebae. The number of peripheral spherules is much smaller than in the trophic nucleus. They lie in the peripheral zone, imbedded in the peripheral ground-plasm which is also greatly reduced in amount. Endosomal spherules, somewhat less refractive than the peripheral spherules, are usually more numerous than in the trophic nuclei, and are much smaller.

During nuclear transformation no great alteration in the cytoplasm occurs. The amount of food decreases, and the cytoplasm is usually completely free from food vacuoles by the end of the nuclear transformation. The nuclear appearance alters comparatively little insofar as the living nuclei are concerned. The more refractive peripheral spherules disappear, but are replaced by endosomal spherules. These are usually quite deliberate in their migration around the central region after division, and are frequently seen surrounding half of the nucleus in a "crescentic" area. The alterations in the central region, as seen in fixed nuclei, are apparently not visible in life. The nuclear membrane becomes much thinner.

After transformation of the nuclei into their new structure, the amoebae remain actively motile for a time. This is followed by a rounding up of the organism, during which the cytoplasm becomes noticeably more dense. At this time the larger inclusions stained by neutral red disappear, although granules appear to occur. There are indications of a reduction in the number of the smaller inclusions, also, but this is not so striking as the disappearance of the larger spherical inclusions. The formation of the cyst wall appears to be a rather slow process during which some cytoplasmic streaming occurs. No other visible activities occurred. It may be that it occurs more rapidly in hosts than it does in depression slide mounts, but no means of determining its speed in the host has been devised. On slides it requires from one to several days for completion.

XVII. THE EARLY PRECYSTIC PHENOMENA

THE APPEARANCE of the nuclei in the early precystic amoeba is quite like that of the nuclei seen in the rapidly dividing "precystic" organisms. Each nucleus is smaller after each division, although the ratio of nuclear mass to cytoplasmic mass appears to be increased during the divisions. The nuclear membrane is rather thin, but reacts to stains and fixatives exactly as the nuclear membrane of the trophic amoeba. It is homogeneous after all fixatives, and, in all but osmic fixations, is acidophilic.

The peripheral zone is restricted in extent. There is a much reduced amount of ground-plasm, which is usually homogeneous or finely reticular after fixation. As in the trophic nucleus, fixation with low grades of acetic fails to preserve the ground-plasm. The basophilic peripheral granules are much smaller in number than in the trophic nucleus. They are present in small numbers during the early precystic period, however, although they appear to become less numerous as the number of nuclei increases. There are a few peripheral spherules in most nuclei, visible after alcoholic or formaldehyde fixation. They are resistant to staining.

The endosomal material is present in the form of tiny spherules which are unstained in Feulgen preparations, but are distinctly basophilic. These small spherules, visible in life, are very rarely fused into true endosomes, although this does occasionally occur in early stages. The occasional nuclei in which endosomes are formed from the endosomal spherules never contain elongated strands, but instead the spherules mass together into spherical clumps which rapidly become smoothly rounded (Fig. 65). The endosomes and the endosomal spherules are well preserved by all of the compound fixatives. Although the spherules are usually attached to the nuclear wall they are sometimes clumped around the central region (Fig. 70). They are sometimes irregular and appear to be less basophilic after alcohol fixation. Although the endosomes were rather poorly fixed in trophic amoebae by glacial acetic acid, this is less noticeable in the precystic amoebae. They are well preserved by glacial acetic acid. The visible differentiation of light-staining and dark-staining substances is not found in the precystic endosomal material. The fact that all of the endosomal material appears to be equally well preserved in glacial acetic acid and 10 per cent acetic acid when the light-staining material is absent supports the view that it is the light-staining material which was poorly preserved in the trophic endosomes by acetic acid. The shorter interphase period may account for the failure of the less basophilic material to form, if the basophilic material is indeed broken down in the interphase stage into the less basophilic vacuolar material.

The central region of the early precystic amoeba is but little altered.

Radii connect the central region to the peripheral region, and in some cases the radii appear to penetrate through the peripheral material and attach to the nuclear membrane. The number of radii is not constant in the precystic amoebae, nor in the trophic amoebae, thus contrasting with the constancy in the number of radii in *Entamoeba histolytica*, reported by Kofoed and Swezy (1925). The central region is usually homogeneous, but in some cases may appear somewhat fibrous. The fibrous consistency is seen most frequently in material fixed in chromic acid or Zenker's fluid. The central region is usually acidophilic, but following a chromic acid or Zenker fixation, it is quite basophilic. This appears to be the result of a mordanting action of the chromic acid rather than the presence of basophilic material not fixed by other reagents. The actual amount of central region material appears to decrease during the several nuclear divisions, but much less than the peripheral material. It is little more conspicuous than in the trophic amoebae, in spite of the smaller amount of obscuring peripheral material. The hyaline body can be found after appropriate fixation. It is more prominent than in trophic nuclei, and is somewhat more resistant to deleterious fixations. Although it cannot be traced throughout the whole interphase, it appears to last during a greater portion of the interphase than is the case in the trophic nuclei.

Early precystic divisions are typically like the trophic divisions. The first division producing four nuclei is rarely exactly synchronous, so that a trinucleate stage is rather common. In these trinucleate forms one nucleus is usually in the early kinetophase condition, while the other two are in the early interphase. The first division seems to be somewhat atypical, especially in some amoebae. Mercier (1910) described a clumping of chromatic constituents together in the binucleate stage to form a transitory karyosome. The further changes of this structure are described as follows (p. 158), "Le caryosome se décompose et donne d'une part les nucleolés et d'autre part un appareil centrosomien (centrosome et sphere) qui est situé dans la zone claire du noyau." This karyosome described by Mercier has not been found, unless he refers to the hyaline body. Occasionally a large endosome formed from several endosomal spherules occurs, but in no case can this be considered as similar to the karyosome mentioned by Mercier. Mercier figures (Fig. 24) a division from the binucleate to the trinucleate stage. He finds a centrosomal granule at each pole and a number of chromatic bodies which extend between the granules. In the material of the present investigation these atypical divisions have occasionally been observed. The normal division figures are characterized by their comparatively round shape and bluntly rounded poles (Fig. 67). No chromosomes could be found in these nuclei. These may have represented nuclei in the so-called "dedifferen-

tiated" stage which were beginning to elongate. In other cases, nuclei dividing in a typical fashion were found.

The tetranucleate organism is capable of undergoing nuclear transformation, but this is apparently a rare occurrence, the change in nuclear structure usually occurring in the 8-nucleated stage. Since the divisions are not wholly synchronous, the number of nuclei do not coincide with the powers of two. In rare cases a full 16 nuclei are formed before transformation occurs.

The precystic divisions following the first one are typical. Endosomal spherules lie in the median part of the elongated nucleus, and the chromosomes are found at the poles (Fig. 68), where they are sometimes clumped in a slightly basophilic mass. In the constricted daughter nuclei, the typical telephase appearance is usually observed (Fig. 69). There are some indications that a reduction in chromosomal material has occurred, for the chromosomal clump is noticeably smaller in size, and attempts to count the chromosomes give consistently lower numbers. Until the number of chromosomes has been definitely determined in the trophic stage, however, no definite meiotic processes can be recognized.

Constriction of the nucleus leads to the late kinetophase reconstruction. The basophilic endosomal spherules, imbedded in the peripheral ground-plasm, lie in a crescentic mass at one pole of the daughter nucleus after the nucleus has rounded up (Fig. 73). At the opposite pole are the chromosomal strands which are slightly basophilic in haematoxylin preparations, but are very clearly basophilic in safranin preparations. The chromosomes are positive to the Feulgen test. The hyaline body may be found at the pole of the dedifferentiating chromosomes, but it is smaller than in the trophic nucleus. The karyolymph sometimes forms a spherical mass between the chromosomes and the peripheral material.

XVIII. NUCLEAR TRANSFORMATION

THE END of the early precystic development during which the increase in number of nuclei was accomplished is marked by a complete alteration in nuclear morphology. The nuclear transformation appears to begin with a gradual increase in the nucleic acid content of the central region, as indicated by the Feulgen reaction. At first the central region is stained a diffuse violet color in Feulgen preparations, but the shade gradually becomes more intense as the transformation of the remaining components advances. It appears that the peripheral spherules disappear at this time, and it is suggested that if they are truly a phosphoglobulin-like substance, they may supply the central region with a phosphorous compound utilized in producing nucleic acid. At one pole of the central region a

small basophilic granule appears. Its position is such that it seems to have been derived from the hyaline body, but it is entirely unlike the hyaline body in its reactions to stains and fixatives. It is clearly distinct from the central granule found in the trophic and precystic nucleus, for this nuclear element can be seen in the center of the central region at the same time that the larger eccentric granule is present (Fig. 71). Morris (1936) says that the "karyosome" or centriole is more conspicuous in the precystic amoeba than in the trophic form. This does not seem to be the case, for the centriole is quite difficult to demonstrate in the precystic amoebae. Morris may possibly have mistaken the eccentric body for the central granule or centriole. The eccentric granule increases in size (Fig. 72) and becomes still more noticeably positive to the Feulgen test at this time. The peripheral material is not greatly altered. The ground-plasm is slowly decreasing in amount and the basophilic endosomes and endosomal material are concentrated into smaller granules which finally become arranged along the inner surface of the nuclear membrane at relatively regular intervals. This occurs at different speeds, so that no definite time for the completion of the redistribution of the peripheral material can be specified. It is usually completed before the central region alterations are completed, but this is not invariably the case.

The eccentric basophilic body becomes altered by its disruption into several distinct granules during later development. This seems to differ somewhat in different fixatives, but the reason for this variation is not wholly understood. With strong alcoholic fixatives the body generally forms a small basophilic circlet (Fig. 76), which is at first undifferentiated and homogeneous along its whole length, but later forms four or five distinct granules, connected by more lightly-staining material (Fig. 77). The circlet is less prominent after Zenker fixation, but usually can be found in favorable cases. In osmic-containing fixatives, however, the circlet is almost invariably lacking. In its place there is a larger eccentric body, from which the four or five granules are formed directly.

The appearance after transformation approaches the morphology of the cyst nuclei, but is very unlike that of the trophic nucleus. The nuclear membrane is comparatively thin. Along its inner surface there are a number of small basophilic granules developed from the endosomal spherules, which are arranged at almost regular intervals. They are negative to the Feulgen test, and have been derived from the peripheral material of the trophic nucleus. The central ground-plasm is acidophilic, and contains a small central granule which is quite inconspicuous, although basophilic. The eccentric basophilic circlet and associated granules are positive to the Feulgen test, and after the completion of the nuclear transformation appear to contain the majority of the nucleic acid found in the nucleus.

XIX. THE LATE PRECYSTIC PHENOMENA

THE NUCLEI may divide after the nuclear transformation, before the formation of the cyst wall, but this does not appear to occur in all cases. This division, when it does occur, is atypical. It is initiated by a transverse division of the basophilic, eccentric circlet (Figs. 77, 78). After division of the circlet, the two halves each unite to form a smaller circlet (Fig. 80) which migrate to opposite poles of the central region. The next step has not been observed, but apparently consists of an elongation of the nucleus and the migration of the daughter circlet to the pole of the nucleus. Once arrived at the poles, the circlets remain in this position, while the elongated nucleus constricts (Fig. 81), forming two daughter nuclei. Chromosomes have never been seen in this type of division. The rarity of the dividing figures suggests that division may be very rapidly completed, or that it is quite rare. It occurs most frequently in precystic amoebae with few nuclei. It is probable that, since nuclei have been seen in the early division stages more frequently than in the later stages, the actual elongation and constriction of the nucleus occurs in a comparatively short space of time. Reconstruction after division leaves the nucleus with a small circlet, about half the size of the normal circlet (Fig. 80).

The nuclei undergo another morphological transition as the cyst wall formation approaches, and the amoeba rounds up and becomes inactive. The cytoplasm acquires an odd striated appearance which has been described by Mercier (1910) and Morris (1936). These investigators also observed that the nuclei migrate to the center of the organism where they form a small clump. The nuclear structure is wholly altered. The interior of the nucleus is filled with a spongy reticulum which bears a large number of granules. In its general appearance it is quite similar to the dedifferentiated stage of the dividing trophic nuclei, from which it differs primarily in that the particles occurring on the spongy net are deeply basophilic and positive to the Feulgen test (Fig. 82). As the nuclei acquire irregular shapes the granules which occur on the reticulum become quite darkly colored by the Feulgen reaction, and the nucleic acid content appears to reach its peak. At no other time during the life cycle, from trophic amoeba to mature cyst, does there appear to be such a high concentration of the nucleic acid. During the succeeding activities the nucleic acid content is rapidly reduced, and it is believed that the nuclei are active in some way during the formation of the cyst wall. Their irregular shape, and their indistinct outlines appear to support this view. Later changes, to be described with the cystic phenomena, suggest that these changes may be considered as early kinetophase activities in part.

XX. THE CYSTIC PERIOD; HISTORICAL REVIEW

WHEN THE deposition of the cyst wall occurring at the end of the precystic period is completed, the amoebae pass into the cystic stage. The wall is thick and hyaline, and quite conspicuous. At this time they begin to pass down to lower parts of the alimentary tract.

Bütschli (1878) was the first to describe the cysts. He mentions thick-walled multinucleate cysts which were probably a part of the life cycle of the amoeba. He noted that the nuclei were much smaller in the cysts, ranging from about 3 to 8 μ .

Schubotz (1905) described the cyst nuclei as varying from about 4 to 6 μ . Each cyst contained from 20 to 30 nuclei. The nuclei were spherical to elliptical, and the central region was much less prominent than in the trophic forms. The cyst nuclei appeared to be finely granular, and few refractive granules occurred along the nuclear membrane. The nuclei usually lay in the hyaline part of the cytoplasm, which became divided into two zones, a finely granular darker part and a hyaline lighter part. He noted that in some cysts nuclei were found lying side by side, with adjacent parts of the nuclear membrane flattened. He believed that this might represent division or copulation. Since there was no reduction in number of nuclei in the older cysts, Schubotz came to the conclusion that these paired nuclei were more probably dividing than copulating. A week in a moist chamber did not bring about any alterations, but cysts from faeces which had been dried showed distinctive differences. The cyst wall, while as thick as in the fresh cysts, was often irregular. The cytoplasm was uniformly granular throughout, as the hyaline protoplasm had disappeared. The nuclei were irregularly distributed over the whole cyst, but differed little or none from the nuclei in the fresh cysts. Although he was unable to bring about development from cysts in feeding experiments he observed a number of very small amoebae (6 to 8 μ) which were characterized by their hyaline cytoplasm and active movements. He believed that these were young *E. blattae*.

Elmassian (1909) studied encystment in the colon of the host and in material forced to encyst by leaving the trophic amoebae in solutions of salt containing the teased apart host colon at 12° C. and at room temperature. At room temperature encystment was rather capricious, but at low temperatures the course of the encystment was slow and many amoebae were still motile after 9 days in salt solution. He found two kinds of cysts, light and dark. The cyst wall was laid down in the uninucleate stage in the case of the dark cyst. Secondary nuclei developed into the cyst nuclei. At the time of their release into the cytoplasm, the secondary nuclei were nearing division, and they formed a primitive spindle on which fine chromatic granules were distributed. The bursting

of the nucleus left a fine chromidial residue, which formed a reticulum throughout the cytoplasm. The secondary nuclei underwent several divisions until their number was considerably increased. In some of the nuclei a halo of chromatic material lay around them which was at first crescentic in shape and then formed distinct granules. He believed that this was a process of chromatin diminution. At this time the nuclei often appeared to be in pairs, which he described as a fusion of gametic nuclei. The contents of the cyst assumed a new form at this time. The nuclei divided, increasing in numbers, but in doing so, decreasing in size, while the cytoplasm separated into light and dark plasms. The granular dark plasm was differentiated from the hyaline light plasm by its affinity for basic dyes, which he considered to be due to the remains of the chromidial net. The cytoplasmic differentiation was lost by the time that the cysts were expelled from the colon. As many as 72 nuclei were found in one cyst. Small chromatic granules occurred at the periphery of the small nuclei found in the ripe cyst. Elmassian believed that there were two divisions involved in cyst formation, the first of which was a true mitosis.

The clear cysts had fewer nuclei. As described in the precystic discussion, they were derived from a binucleate precystic form, which secreted a cyst wall. The two nuclei were characterized by a very thin nuclear membrane enclosing a fine reticulum on which there were a large number of fine chromatic granules. The two nuclei prepared to divide, elongating and assuming a characteristic spindle shape. A chromatic mass occurred at each pole of the elongated nuclei. The two spindles constricted in the center, producing four spindles, which changed shape somewhat, and then divided into 8 nuclei. Two more divisions took place, producing 32 nuclei in the mature light cysts. The spindles observed during the divisions involved in the cyst development were characterized by small granular chromosomes. There was no centriole. The irregular chromatin occurring at the poles of these spindles, Elmassian believed to be something other than chromosomes.

Elmassian was of the opinion that the light cysts represented a schizogonic cycle, while the dark cysts, in which the paired nuclei fuse, represented a sporogony, similar to that occurring in the Sporozoa.

Janicki (1909) noted that cysts were usually formed from small amoebae with 8 nuclei. Mitotic divisions similar to those found in the trophic amoebae occurred in precystic development, but cyst divisions were different. The karyosome initiated division by elongating and becoming slender. Two centrioles appeared at the poles of the elongated karyosome, which Janicki was inclined to believe originated by the division of a single centriole. No structure connecting the two centrosomes was present. A small amount of indistinct chromatin was

present at that time. Within the nuclear membrane a spindle was formed. An equatorial plate stage was easily found at the time that the nucleus was spindle-shaped. There were six spherical chromosomes which moved to the poles and gathered together in rather indistinct masses. The karyosome reappeared in the resting stage, surrounded by granular chromatin. Up to the stage with 8 or 16 nuclei the divisions were more or less synchronous. Cysts with up to 30 nuclei were found.

Mercier (1910) considered encystment as a process allied with gametogenesis. The cyst stage was reached when the amoebae were in the 8-nucleated stage in most cases. As the cyst wall began to form the nuclei were clumped in the center of the organism. The cytoplasm was distinctly striated at that time, but the striae disappeared very soon after the cyst wall was completed. When the cytoplasm regained its homogeneous condition the 8 nuclei divided more or less synchronously. The divisions were mitotic, but the nuclear membrane persisted through this and succeeding divisions. The later divisions were more difficult to follow because of the small size of the amoebae. Chromidia occurred in the cytoplasm, derived from the precystic reduction process. Cysts so formed were passed out with the faeces.

Morris (1936) was the last to undertake a study of encystment. He observed that the nuclei of the precystic amoebae migrated to the center of the body at the time of cyst wall formation. The cytoplasm became more dense as the cyst wall was secreted. After the cyst wall was formed one nuclear division followed immediately. The small size of the nuclei made it impossible to study the division satisfactorily but he observed that there were indications that it was atypical. After this division no further nuclear changes occurred, and the two cytoplasmic phases separated into a denser, hyaline material and a more fluid granular material occurring in the form of large vacuoles. The ripe cysts passed out of the host in the faeces and infected new cockroaches.

XXI. APPEARANCE OF FRESH CYSTS

THE CYSTS vary in size from about 20 μ to almost 50 μ . They are very easy to recognize because of their refractivity, and may be located readily even under low magnifications. The cyst wall is relatively thick, sometimes attaining a thickness of 4 to 5 μ , but usually measuring 2.5 to 3.5 μ . It is refractive and hyaline, and is closely pressed against the cytoplasm lying within it. The outer surface of the cyst wall is relatively smooth in fresh cysts, but, as pointed out by Schubotz (1905), it becomes quite irregular in cysts which have been dried in faeces. The differentiation of the hyaline and granular plasma is quite difficult in living cysts but can

be made out with careful study. The nuclei are quite small, and in many cysts are invisible in life. The smallness of the nuclei, and the fact that their refractive index approaches that of the cytoplasm makes it impossible to study them satisfactorily in life.

XXII. STUDY OF FIXED AND STAINED CYSTS

THE FIXED and stained cysts undergo some shrinkage during treatment, but fall in the same size range as the living ones. The cytoplasm is frequently somewhat basophilic, and it is extremely difficult to accomplish satisfactory differentiation.

The cyst wall is quite heavy and shows indications of stratification in many cases, especially after sectioning. The cyst wall is quite resistant to staining with basic dyes, and is lightly stained or unstained with the cytoplasmic dyes. The cytoplasm at the time the cyst wall is formed is striated. As described by Morris, the cytoplasm becomes homogeneous after the deposition of the cyst wall. At this time it is hyaline and appears to be quite dense. During later development vacuoles of a granular, more basophilic plasma appear in it. These seem to appear near the periphery first, and fuse together, later migrating to the center of the cyst. The mature cyst usually contains from one-half to one-third granular plasma. In older cysts this may be even more pronounced, and Schubotz (1905) found that in week-old dried cysts all of the cytoplasm is granular. This suggests that Elmassian's view that the granular part of the cytoplasm represents chromidia is very doubtful. Another viewpoint is expressed by Morris (1936, p. 235): "At the close of the cystic nuclear division, the two cytoplasmic phases, described earlier in the active adult amoeba, separate from each other; the denser, less fluid portion forming a continuous matrix wherein the nuclei rest, while more fluid material forms a series of large vacuoles at the periphery of the cyst." It seems much more probable, in view of the fact that the whole of the cytoplasm is at first homogeneous, and gradually becomes divided into a hyaline and a granular type of plasma, that the two were not present at first as two distinctly different types of plasma. The writer is inclined to believe that there is a gradual formation of the granular from the hyaline plasma, which may, possibly, result from certain metabolic activities which occur. At any rate, the hyaline plasma may be entirely converted into granular plasma after a period of drying. As observed by all previous investigators who have studied the cysts, the cyst nuclei appear to prefer the hyaline plasma.

During the late stages in the cyst wall formation the nuclei are irregular and somewhat elongate. In a few cases the nuclei begin to become

regular in outline while the cyst wall is quite thin, but this does not appear to be general. After the cyst wall is completely formed, the nuclei regain their regular outline, and appear as somewhat elongated, usually bluntly pointed nuclei (Fig. 83). The thin acidophilic nuclear membrane contains an acidophilic ground-plasm, which in some cases appears to have formed a spindle. In no case have spindle fibres been seen, however, and if the spindle occurs it is quite indefinite. Arranged in a single girdle around the center of the nucleus lie a number of granules which are intensely basophilic and react well to the Feulgen test. These granules are arranged in rows parallel to the long axis of the nucleus. Although they are not exactly like the chromosomes in the trophic nucleus in their derivation or in their appearance, their obvious relation to division processes has induced the writer to apply the term chromosome to them. They divide into two groups which move toward the poles. Whether this is accompanied by a splitting of each granule has not been determined. During the migration period the rows of granules are irregular and become indistinguishable. Janicki's (1909) metaphase of the cyst nuclei probably corresponds to these atypical spindles and chromosomal granules. The spindle is elongated during the migration of the granules to the poles, and a constriction divides the spindle into two daughter nuclei. Division of spindles into daughter spindles, as described by Elmassian (1909) has not been observed.

The cyst nuclei arising from these spindles are characteristic in shape and structure. They are spherical and rather small, averaging between 4 and 5 μ in diameter. The nuclear membrane is quite thin, and within it lies an area of basophilic material which is in contact with the membrane along its whole periphery. In some cases this is irregular in distribution, forming a crescentic mass at one side of the nucleus. This seems to be identical with the "halo" mentioned by Mercier (1910) and Elmassian (1909). Insofar as could be determined the nucleus does not extrude chromatin into the cytoplasm. Within the basophilic area there are usually several discrete chromatic granules which appear to be derived from the endosomal granules of the precystic nucleus (Fig. 90). Within the peripheral basophilic zone there is a narrow light-staining region containing a small basophilic granule in the center of it (Fig. 90). This is apparently identical with the centriole observed in the trophic nuclei.

Two other types of nuclear division were found. In several cysts a division typically like the trophic divisions was found. In these nuclei the chromosomes are apparently quite similar in nature to those found in the trophic form. They migrate to the poles of the elongated nucleus, and between the two clumps of chromosomes there is an area of dark-staining granules (Fig. 84). The question as to whether the division figure repre-

sents a second cystic division will be discussed later. The chromosomes found at the poles of such dividing nuclei are more basophilic than the trophic ones. Definite basophilic granules stained with haematoxylin occur in them. Like the first division, it is synchronous.

There is a third type of division figure which is quite rare. It was observed in two small cysts. The nuclei were much elongated and had begun to constrict in the median line. There were vague signs of a spindle, as in the division figures first mentioned in this section, but no visible spindle fibres occurred. Basophilic structures in these nuclei were limited to four granules at the poles of the nuclei, which were almost exactly like the atypical precystic division (Figs. 85, 86). Chromosomes and endosomal spherules appeared to be wholly absent. The possible significance of this type of division is not known.

The question as to whether there is more than one division in cystic development has not yet been definitely settled. It appears certain that there is more than one division, for although but few of the precystic amoebae have more than 16 nuclei in them, and most contain about 8 nuclei, the cysts almost invariably contain at least 32 nuclei, and may have as many as 72. Morris (1936) says that the precystic amoebae contain from 4 to 16 nuclei and that the cysts may contain from 64 to 72 nuclei. As to the methods of increase of nuclei after the first cystic division, Morris leaves us in doubt, and although a single nuclear division will not suffice to increase the nuclei from the average precystic to the average cystic numbers, he says (p. 235), "A final nuclear division immediately follows encystment," and again "Mercier believed that more than one postencystment division might occur, but the present observations do not confirm this view." It seems quite possible that the first nuclear division is followed by the type of division described as similar to the trophic divisions. It was interesting to notice that although the chromosomes could not be accurately counted because of their small size and the poor differentiation which was frequently obtained, there seems to be more than half as many as in trophic divisions. This may indicate that no meiotic phenomena have occurred, or that nuclear fusion occurs in the cyst as believed by Elmassian. No evidence on either point is at hand.

Some evidence for an amitotic division of cyst nuclei has been discovered. In several cysts a few nuclei were found in which the nuclei were pear-shaped and appeared to have recently constricted (Fig. 88). There were no signs of chromosomes or spindle, and it resembled an amitotic division in all respects. Variable size among the cystic nuclei has been observed in many cases, suggesting that there may be occasional nuclear divisions following the synchronous mitotic ones (Fig. 87).

At the time of cyst wall formation the nucleic acid content of the cystic nucleus is very high. During the first division of the cystic nucleus the granules lying on the spindle are colored a deep violet red by the Feulgen test. The second type of division is also a period when the amount of nucleic acid is quite high. After this second division, however, the nuclei gradually become less deeply colored, and by the time that the cyst has reached maturity the nuclei are almost completely negative to the Feulgen test.

XXIII. SUMMARY

(1) THE CYTOPLASM of *Endamoeba blattae* is differentiated into ectoplasm and endoplasm. The relative amount of the former is usually greater in less active organisms. The endoplasmic streaming is fountain-like in active amoebae, the central axial stream breaking anteriorly into superficial currents which stream back beneath the surface. In at least some amoebae there appears to be a gelation about one-third to one-fourth of the way back from the anterior end, and a posterior region where solation occurs. When the organism is among detritus, and in other cases, gelation and solation may not occur. Other types of pseudopodial formation occur and are discussed briefly.

(2) The cytoplasm contains a number of small thread-like mitochondria which may be related to the food vacuoles. These are not noticeably altered during the development of the precystic amoebae.

(3) Inclusions which are osmiophilic and argentophilic occur and are stained by neutral red. They fall into two groups, one larger type consisting of a chromophobic core and a chromophilic cortex. The cortical portion, when vitally stained, consists of a number of small granules, apparently identical with the second type of inclusion occurring in the cytoplasm; small, intensely chromophilic granules, almost uniform in size. The spherules are sometimes in contact with the food vacuole wall. The function of these inclusions is discussed briefly, without drawing any definite conclusions. The spherules are reduced in number in the precystic amoebae, although the granules are apparently not affected.

(4) The trophic interphase nucleus is a large heavy-walled structure with a characteristic concentric arrangement of parts, involving a peripheral zone and a central region. In living nuclei the peripheral region consists of a homogeneous ground-plasm enclosing larger peripheral spherules which are highly refractive, and smaller less refractive granules. In fixed nuclei the peripheral ground-plasm appears as a finely reticular or homogeneous region which contains smaller basophilic granules and larger spherules which are resistant to staining with acid and basic dyes. At the inner margin of the peripheral zone there are a variable number of

endosomes composed of a basophilic outer and a lightly-staining inner region, containing a small basophilic central granule. The acidophilic central mass is transparent in living nuclei and is usually reticular, but may be homogeneous, in fixed nuclei. At the center of this central region a basophilic centriole is found in many nuclei.

(5) During division the central region becomes more basophilic and a small amount of nucleic acid, as determined by the Feulgen nucleal reaction, appears in it. At this time the centriole is frequently double. The nucleic acid content of the central region increases as the chromosomes appear. The chromosomes are beaded strands which shorten and become condensed into homogeneous strands which have a high nucleic acid content. Just before the chromosomes migrate to the poles the endosomes are broken down and the remaining basophilic material forms small basophilic endosomal spherules. Some of the peripheral granules may also form similar endosomal spherules. The concentric arrangement is disrupted as the endosomal spherules migrate to the center of the elongating nucleus, where they become arranged in longitudinal rows. The chromosomes migrate to the poles and form a rosette, after which the nucleus constricts and forms two daughter nuclei. The chromosomes mass together as they dedifferentiate and form a new central region which rapidly loses its nucleic acid and affinity for basic dyes. The chromosomal dedifferentiation is associated with the appearance of a hyaline body which is at first basophilic, but gradually becomes less basophilic after the new central region is formed, finally disappearing during the middle interphase.

(6) The interphase nucleus undergoes an alteration with respect to endosomal appearance, thought to be associated with metabolic activities. The early elongated endosomal anlage are formed from the endosomal spherules and a light-staining substance, the derivation of which is unknown, at the time that the chromosomes dedifferentiate. They migrate around the central region with the peripheral ground-plasm to renew the concentric arrangement of the nucleus. The early beaded appearance is supplanted by a homogeneous condition, and the strands first become sinuous, and then shorten and become straighter, finally assuming a cuboidal or spherical shape. After the spherical shape is acquired the endosomes differentiate into a basophilic cortex and light-staining inner region.

(7) The nuclear membrane is composed of a protein substance which is apparently in the form of a rather concentrated colloid, possibly mixed with a non-protein substance. The chemical nature of the nuclear elements is quite uncertain, but an attempt to throw some light on their composition is made.

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PLATES

NOTE: All figures are made from camera lucida drawings, and are magnified 1450 times. Leitz oil immersion 1/12; ocular 4.

PLATE I

- FIG. 1. Late kinetophase. Endosomal anlage migrating around developing central chromosomal mass. Gilson-Carnoy, haematoxylin, orange G.
- FIG. 2. Late kinetophase. Slightly later stage than Fig. 1. Gilson-Carnoy, haematoxylin, orange G.
- FIG. 3. Early interphase. Continuous peripheral region; endosomal anlage becoming homogeneous. Gilson-Carnoy, haematoxylin, orange G.
- FIG. 4. Early interphase. Hyaline body at pole of developing central region. Flemming, safranin.
- FIG. 5. Early interphase. Destained more than usual. Note rows of endosomal spherules and absence of peripheral granules. Gilson-Carnoy, haematoxylin.
- FIG. 6. Early interphase. Endosomal material not formed in straight lines. Gilson-Carnoy, haematoxylin.
- FIG. 7. Middle interphase. Endosomes in the form of sinuous strands. Surface view of nucleus. Gilson-Carnoy, haematoxylin.
- FIG. 8. Middle interphase. Endosomes contracting. Gilson-Carnoy, haematoxylin.
- FIG. 9. Middle interphase. Endosomal spherules still visible, due to transparency of stain. Hyaline body becoming less basophilic. Flemming, safranin.
- FIG. 10. Middle interphase. Sinuous endosomes. Flemming, haematoxylin.
- FIG. 11. Middle interphase. Endosomes gathering at margin of the peripheral zone. Gilson-Carnoy, haematoxylin.
- FIG. 12. Middle interphase. Sinuous endosomes, homogeneous and at their definitive position. Hyaline body gone. Flemming, safranin.
- FIG. 13. Middle interphase. Endosomes oriented in parallel direction. Gilson-Carnoy, haematoxylin.
- FIG. 14. Late interphase. Differentiated less than usual. Note the granular peripheral region and irregular endosomes. Gilson-Carnoy, haematoxylin.
- FIG. 15. Late interphase. Endosomes spherical; hyaline body still present. Flemming, safranin.
- FIG. 16. Late interphase. Endosomes cuboidal. Gilson-Carnoy, haematoxylin.
- FIG. 17. Late interphase. Endosomes spherical; hyaline body not present. Flemming, safranin.
- FIG. 18. Late interphase. Endosomes spherical, showing division into two types of substance. Carnoy, haematoxylin.



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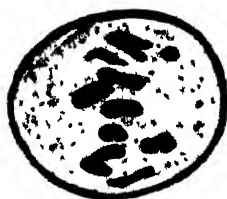
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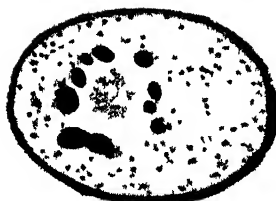
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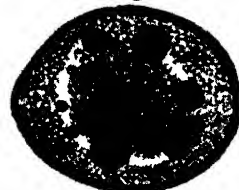
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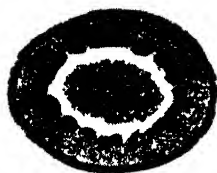
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PLATE II

- FIG. 19. Late interphase. Note poor preservation of endosomes. Carnoy, haematoxylin.
- FIG. 20. Late interphase. Schaudinn, haematoxylin.
- FIG. 21. Early kinetophase. Chromosomal strands appearing in the central region; centriole double. Gilson-Carnoy, haematoxylin.
- FIG. 22. Early kinetophase. The "dedifferentiated stage." Endosomes breaking down to form endosomal spherules. Gilson-Carnoy, haematoxylin.
- FIG. 23. Early kinetophase. Later stages of endosomal disruption. Gilson-Carnoy, haematoxylin.
- FIG. 24. Middle interphase. Endosomal spherules median; chromosomes appearing at edges of girdle of endosomal material. Gilson-Carnoy, haematoxylin.
- FIG. 25. Middle interphase. Chromosomal strands in central region; centriole double. Gilson-Carnoy, haematoxylin.
- FIG. 26. Middle kinetophase. Peripheral view of nucleus shown in Fig. 25. Girdle of endosomal spherules. Gilson-Carnoy, haematoxylin.
- FIG. 27. Middle kinetophase. Chromosomes at poles; endosomal material forming a basophilic reticulum. Gilson-Carnoy, haematoxylin.
- FIG. 28. Middle kinetophase. Chromosomes at poles; endosomal spherules discrete, not forming a reticulum. Flemming, safranin.
- FIG. 29. Late kinetophase. Beginning of nuclear constriction. Gilson-Carnoy, haematoxylin.
- FIG. 30. Late kinetophase. Slightly later than Fig. 29. Gilson-Carnoy, haematoxylin.
- FIG. 31. Late kinetophase. Daughter nucleus after constriction. Gilson-Carnoy, haematoxylin.
- FIG. 32. Late kinetophase. Daughter nucleus beginning to develop toward the interphase. Beginning of the peripheral migration.
- FIG. 33. Nucleus immediately after fixation with Flemming's fixative.
- FIG. 34. Nucleus treated with methyl green.
- FIG. 35. Nucleus immediately after fixation with dioxane.
- FIG. 36. Nucleus immediately after fixation with osmic tetroxide.
- FIG. 37. Living nucleus, early interphase.
- FIG. 38. Same nucleus as Fig. 37, immediately after treatment with absolute alcohol. Note hyaline body at pole.



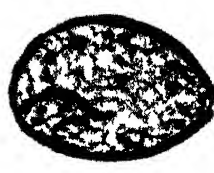
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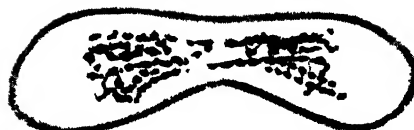
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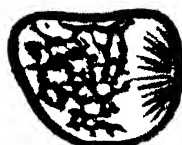
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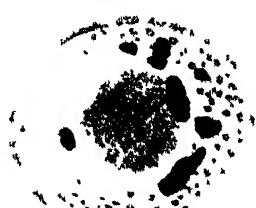
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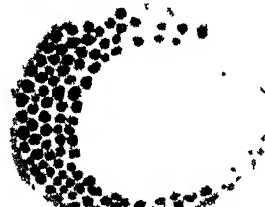
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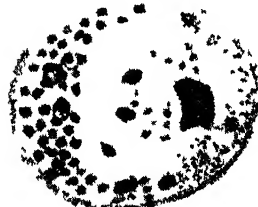
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PLATE III

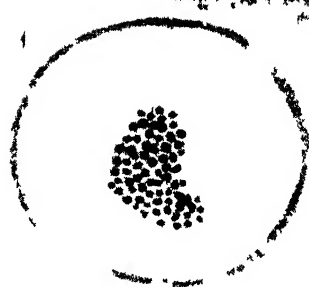
- FIG. 39. Section through whole amoeba. Gilson-Carnoy, haematoxylin.
- FIG. 40. Nucleus 7 minutes after being placed in 10 per cent potassium chloride.
- FIG. 41. Same nucleus after 12 minutes in 10 per cent potassium chloride.
- FIG. 42. Nucleus immediately after fixation with Gilson-Carnoy and staining with methyl green.
- FIG. 43. Peripheral region of nucleus fixed in cold absolute alcohol. Unstained peripheral spherules present. Haematoxylin.
- FIG. 44. Early kinetophase nucleus fixed in cold absolute alcohol. Chromosomal strands visible in central region. Haematoxylin.
- FIG. 45. Middle interphase nucleus fixed in hot absolute alcohol. Endosomes poorly preserved; central region homogeneous. Haematoxylin.
- FIG. 46. Peripheral region of nucleus shown in Fig. 45.
- FIG. 47. Dividing nucleus fixed in 70 per cent alcohol. Shape irregular due to shrinkage. Haematoxylin.
- FIG. 48. Late kinetophase nucleus fixed in hot absolute alcohol. Chromosomes unstained. Feulgen.
- FIG. 49. Nucleus fixed in 10 per cent acetic acid. Endosomes and peripheral granules well preserved. Haematoxylin.
- FIG. 50. Reorganizing nucleus fixed in 10 per cent acetic acid. Chromosomes well preserved. Haematoxylin.



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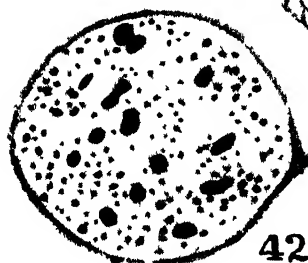
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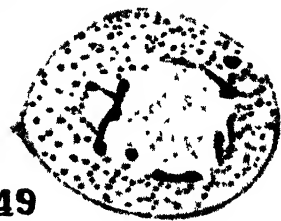
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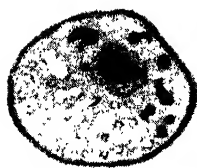
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PLATE IV

- FIG. 51. Nucleus fixed in hot glacial acetic acid. Endosomes incompletely preserved. Haematoxylin.
- FIG. 52. Nucleus fixed in cold glacial acetic acid. Centriole present in homogeneous central region. Haematoxylin.
- FIG. 53. Nucleus fixed in cold glacial acetic acid. Endosomes fused. Haematoxylin.
- FIG. 54. Nucleus fixed in hot formalin. Peripheral spherules and endosomes well preserved. Haematoxylin.
- FIG. 55. Dividing nucleus fixed in hot formalin. Chromosomes indistinguishable as such, but region well stained. Feulgen.
- FIG. 56. Nucleus parasitized by *Nucleophaga* fixed in hot formalin. Haematoxylin.
- FIG. 57. Early kinetophase nucleus fixed in 1 per cent chromic acid. Haematoxylin.
- FIG. 58. Interphase nucleus fixed in 1 per cent chromic acid. No differentiation of peripheral and central ground-plasms. Haematoxylin.
- FIG. 59. Late kinetophase, trophic nucleus. Gilson-Carnoy, haematoxylin.
- FIG. 60. Late kinetophase, trophic nucleus. Gilson-Carnoy, haematoxylin.
- FIG. 61. Late kinetophase, trophic nucleus approaching the precystic condition. Gilson-Carnoy, haematoxylin.
- FIG. 62. Late kinetophase, trophic nucleus nearing precystic condition. Note chromosomes forming reticulum and segregation of peripheral and central materials. Gilson-Carnoy, haematoxylin.
- FIG. 63. Late kinetophase nucleus just before the precystic condition is reached. Very small amount of peripheral material. Gilson-Carnoy, haematoxylin.
- FIG. 64. Late kinetophase, precystic amoeba, binucleate. Gilson-Carnoy, haematoxylin.
- FIG. 65. Interphase, binucleate precystic amoeba. Endosomal material scarce. Small amount of food in cytoplasm. Gilson-Carnoy, haematoxylin.
- FIG. 66. Trinucleate precystic amoeba. Nuclei preparing to divide; almost no food in cytoplasm. Gilson-Carnoy, haematoxylin.
- FIG. 67. Dividing precystic nucleus. Mercuric chloride, haematoxylin.
- FIG. 68. Dividing precystic nucleus. Bouin, haematoxylin.



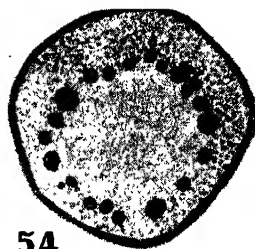
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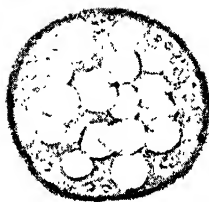
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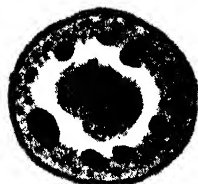
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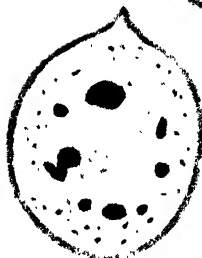
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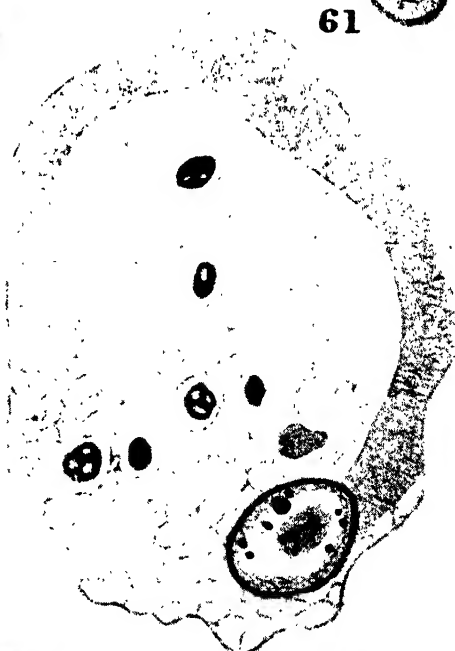
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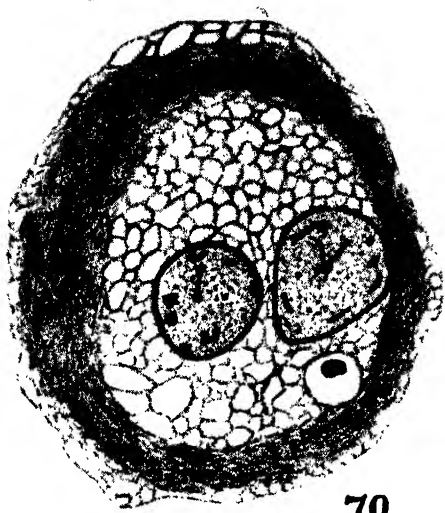
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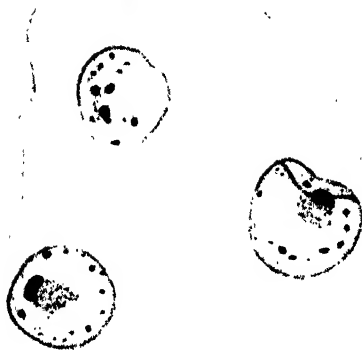
PLATE V

- FIG. 69. Early precystic divisions, late kinetophase. Gilson-Carnoy, haematoxylin.
- FIG. 70. Precystic interphase, before nuclear transformation. Gilson-Carnoy, haematoxylin.
- FIG. 71. Beginning of nuclear transformation. Appearance of eccentric granule. Gilson-Carnoy, haematoxylin.
- FIG. 72. Nuclear transformation. Enlargement of the eccentric granule. Flemming, safranin.
- FIG. 73. Nuclear reconstruction before transformation. Flemming, safranin.



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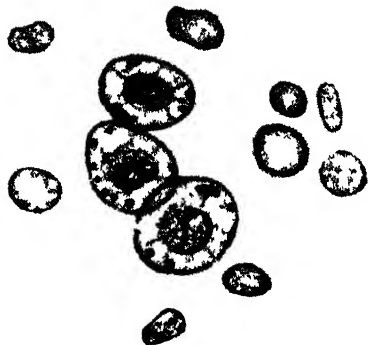
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PLATE VI

- FIG. 74. Precystic amoeba stained with neutral red. Chromophilic granules present, but none of the larger spherical inclusions. Food vacuoles lacking.
- FIG. 75. Nuclear transformation. Formation of the circlet. Flemming, safranin.
- FIG. 76. Precystic amoeba after completion of nuclear transformation. Gilson-Carnoy, haematoxylin.
- FIG. 77. Division of the circlet. Gilson-Carnoy, haematoxylin.
- FIG. 78. Division of the circlet. Zenker, haematoxylin.



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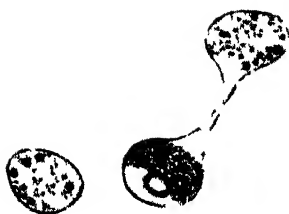
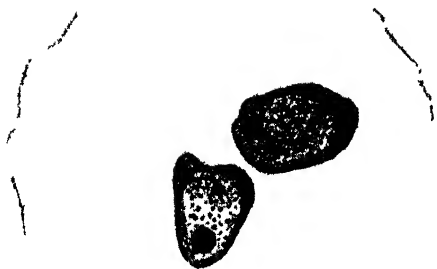


PLATE VII

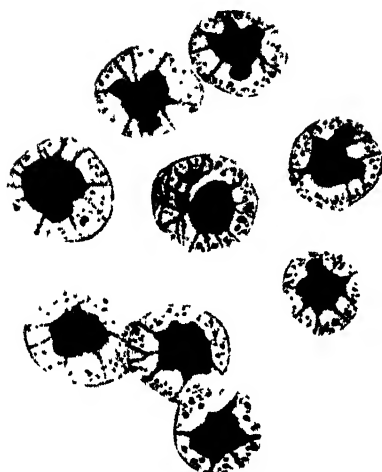
- FIG. 79. Circlet migrating to poles of central region. Gilson-Carnoy, haematoxylin.
FIG. 80. Nuclei after division in late precystic period. Gilson-Carnoy, haematoxylin.
FIG. 81. Late precystic division figure. No chromosomes, circlet at pole. Gilson-Carnoy, haematoxylin.
FIG. 82. Nucleus at time of cyst wall formation.
FIG. 83. Nuclear appearance at time of cyst wall formation. Flemming, safranin.



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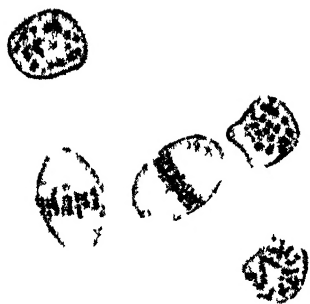


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PLATE VIII

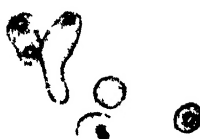
- FIG. 84. Nuclear division immediately after cyst wall formation. Gilson-Carnoy, Feulgen.
- FIG. 85. Cystic division resembling trophic division. Gilson-Carnoy, haematoxylin.
- FIG. 86. Cystic division resembling late precystic division. Bouin, haematoxylin.
- FIG. 87. Next section of same cyst. Bouin, haematoxylin.
- FIG. 88. Cyst with different-sized nuclei. Mercuric chloride, haematoxylin.
- FIG. 89. Mature cyst nuclei. Amitotic (?) division of nuclei. Gilson-Carnoy, haematoxylin.
- FIG. 90. Mature cyst. Hot glacial acetic acid, haematoxylin.
- FIG. 91. Mature cyst. Gilson-Carnoy, haematoxylin.



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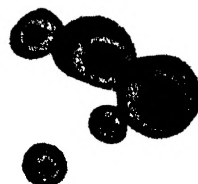
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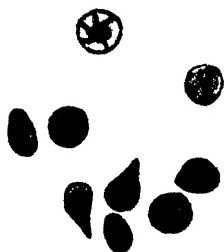
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